# PHYSICO-CHEMICAL CONDITIONS AND BENTHIC COMMUNITY DYNAMICS IN FOUR SOUTH WESTLAND STREAMS.

---

A thesis

submitted for the degree of

Doctor of Philosophy in Zoology

in the

University of Canterbury

by

**ANNE K. GRAESSER**

---

University of Canterbury

1988

# CONTENTS

## ABSTRACT

Physico-chemical characteristics and benthic ecology of four small, stony, brownwater streams in South Westland, New Zealand were investigated between November 1984 and November 1986. Streams were in a high rainfall region (*ca.* 5 m per annum) and had low pH (4.5-6.5), alkalinity and conductivity but relatively high DOC (4-9 $mg.l^{-1}$). Discharge responded rapidly to frequent rainfall events, increasing DOC and lowering pH, alkalinity and conductivity.

Epilithic biomass on tiles was always low (TOC< 200 $ug.cm^{-2}$). Non-algal biomass increased rapidly and was subsequently colonized by bacteria, fungi and algae. Algal composition differed among streams, but not seasonally. Field experiments demonstrated that permanent inundation affected biomass and composition and that invertebrate grazers could reduce biomass.

Amount of detritus (> 0.25 mm) in the streambeds was low (< 60 $gAFDW.m^{-2}$), patchily distributed and occurred non-seasonally.

Eighty-seven invertebrate taxa (including 27 Trichoptera, 18 Plecoptera, 15 Diptera) were recorded. The mayfly *Deleatidium* and the family Chironomidae numerically dominated all streams throughout the year, whereas over $^{2}/_{3}$ of the other taxa were rare (< 1% of numbers). Faunal densities were moderately low (400-1300 $m^{-2}$) as was production of six major insect taxa calculated by the size frequency method (SFM) and Hopkins' method (HM). Although HM has been used infrequently, it gave similar results to SFM and requires less data analysis. All six taxa had poorly synchronized life histories (difficult to interpret; apparently all univoltine). Low drift rates were dominated by terrestrial insects, *Deleatidium* and Chironomidae. Drift densities were negatively correlated with discharge, which suggests that insects may actively avoid drifting when flow increases.

Of the four, Noone Creek had the greatest epilithic algal diversity, invertebrate richness and flow continuity (*ie.* regularly channelled flow). It is hypothesized that this latter factor may account for the high biotic diversity. Stream faunas could be described as "determinate" assemblages (Lake & Barmuta 1986) whose populations were highly resistant and resilient to physical disturbances.

Chapter One

# GENERAL INTRODUCTION

The main objective of my research was to examine the role of environmental stability in regulating the dynamics and production of stream invertebrate assemblages. In order to evaluate the results, it has been necessary to consider them within the framework of current (and past) community theory, a conceptually difficult and often confusing field. This introductory chapter is included to provide the reader with an outline of developments in this challenging area, both in general and more specifically with respect to stream ecology, and to provide the context within which my research was undertaken and developed.

## A. Community ecology

A long-standing debate amongst ecologists concerns the nature of "biological communities", which have been broadly defined as any assemblage of populations of living organisms in a prescribed area or habitat (Krebs 1985). However, this definition does not address the question as to whether such an assemblage is an organized collection of species that recurs in time and space, or a random collection of populations with minimal functional integration.

Clements (1916) viewed biological assemblages as "super-organisms". He proposed that the dynamic stability of the assemblage was self-regulated by the component species and that each species present influenced the functioning of the assemblage. This view was strongly opposed by Gleason (1926) who maintained that assemblages were merely

composed of autonomous populations of organisms that happened to be found in the same geographical area. Support for the latter individualistic assemblage concept (or a compromise leaning towards it) has strengthened over the years (McIntosh 1980, Colwell 1985) as researchers have shown the great diversity, variation and heterogeneity of many biological assemblages. However, many ecological theories concerning maintenance of assemblage structure and diversity are still based upon the view that assemblages are functional entities (Richardson 1980, Colwell 1985). In fact, the individualistic and organismic concepts represent the extremes of assemblage organization, and are in themselves, of little real interest to biologists, unless they build upon current ecological thinking by highlighting general relationships among assemblage components.

For some time, the attention of ecologists has focused on the processes capable of regulating the structure and organization of "multi-species" assemblages. It has been maintained that the stability of an assemblage increases as its complexity increases, that is, as the number of species, and the number of interactions among them becomes greater (Elton 1958, MacArthur 1955). Essentially, an increase in the number of links between species in an assemblage can be seen to function as an important stability increasing factor. Gardner & Ashby (1970) and May (1972) questioned the mathematical basis of this hypothesis, however, and showed through simulation modelling that complex assemblages (ie. many interacting species of predator and prey) could be even more unstable than simple ones.

To-date, studies on stability-complexity relationships have generally been theoretical in nature and few field studies have examined such questions (Pimm 1984, McNaughton 1988). A common problem in applying

mathematical models to ecological systems is measuring parameters in ecological terms that are compatible with specifications of a model (McNaughton 1988). The many different meanings of "complexity" and "stability" used when considering this subject have confused biologists (see Pimm 1984 for a thorough review).

Numerous hypotheses have been put forward to explain the relationships among diversity, complexity, stability and productivity of biological assemblages (see reviews by Pianka 1966, 1976, Menge & Sutherland 1976, Connell 1978). Environmental stability and predictability are often considered to be important determinants of biological diversity, and in physically stable environments, it might be expected that resources would be partitioned and utilized efficiently by species with narrowly defined requirements (MacArthur & Levins 1964, Schoener 1974).

Traditionally, tropical ecosystems such as rainforests and coral reefs have been seen as diverse systems with marked assemblage constancy, but as mentioned earlier, mathematical explorations have cast doubt on the reality or universality of this theoretical condition. The high diversity of tropical assemblages is thought to be strongly influenced by their high productivity, or rather by the high level of solar input as well as weak seasonality and high environmental predictability (Connell & Orias 1964).

Sanders (1969) proposed that the underlying cause of high species diversity in marine benthic assemblages was the predictability of stable environmental conditions over long periods of time. There now seems to be a general consensus that environmental predictability is more important than productivity for the regulation of diversity, although under certain conditions even high predictability cannot compensate for

low productivity. For example, in underwater caves in the tropics, there is little biomass to become diversified (Poulsen & Culver 1969).

Assemblage diversity in ecosystems such as tropical rainforests, could reflect the high degree of spatial heterogenity of such environments and not necessarily environmental stability (MacArthur & MacArthur 1961, MacArthur 1964), and Connell (1978) even suggested that biological assemblages should be less diverse in highly stable environments where biological interactions are most likely to influence their structure (Peckarsky 1983a).

Until recently, many ecologists assumed that natural biological assemblages were at or close to equilibrium with respect to the carrying capacity of their environments, that is, that assemblages were composed of species whose populations fluctuated in size and were compensated for by changes in densities of other species (Cody 1974, Pianka 1976). In harsh or physically unstable environments, however, resource levels and environmental conditions are known to severely limit the sizes of populations of co-existing bird species, and result in loosely structured assemblages (Wiens 1974, 1977). Whether equilibrium populations even exist under nominally "stable" conditions has been called into question by Wiens & Rotenberry (1980) and Wiens (1984), and even if they do they are very difficult to identify in nature (Wiens 1984, Lake 1986).

Moreover, the discrepancy between mathematical definitions of equilibrium and non-equilibrium and their common biological usage in the literature has been pointed out by Grossman (1982) and Lake (1986). Grossman (1982) coined the terms "deterministic" and "stochastic" to describe organization of fish assemblages over time (Grossman 1982, Grossman *et al.* 1982) and his work stimulated useful discussion about the

appropriate methods for assessing assemblage structure (Herbold 1984, Rahel *et al.* 1984, Yant *et al.* 1984, Ross *et al.* 1985).

In a review of stream management and ecological theory, Lake (1986) argued convincingly that "an assemblage with a predictable structure in terms of species composition, may appear to be deterministic, but may not in fact be at equilibrium". According to Lake (1986) assemblages found in predictable environments may respond in a highly predictable or "determinate" way to environmental conditions and give rise to assemblages with both high persistence and resistance to perturbation. In fact, assemblages responding to stochastic environmental conditions, may be more appropriately termed "indeterminate" than "stochastic" as the dictionary definitions of "determinate" and "indeterminate" aptly describe these extremes of assemblage structure (Oxford English Dictionary 1984).

A number of fundamental problems are central to this ongoing controversy in ecology regarding assemblage organization: the scale at which stability is being assessed, ie. the spatial environmental scale and/or the size of population or assemblage groups, and the methodology and terminology used for investigating assemblage structure. Webb *et al.* (1972) found that in tropical rainforests the size of a patch influenced the importance of chance in determining patch colonization dynamics. On small scales, the effect of chance may override the effects of biological association and stochastic factors may become most important in determining assemblage composition (Grieg-Smith 1983).

Neutral or random models have recently been developed to test previously accepted ecological theories concerning the influence of biotic interactions on supposedly "deterministic" assemblages. For example, Caswell (1976) used neutral models as a reference scale to

estimate the effect of biological interactions on assemblage structure. He formed neutral distributions of relative abundances among a group of species, assuming no biological interactions among them, and then compared the distributions with real assemblages of birds, fishes, insects and plants in tropical and temperate zones. Real assemblages were apparently less diverse than his "neutral" distributions, and the discrepancies were greatest in the tropics where more species are thought to co-exist because of intense biotic interactions (Sanders 1969, MacArthur 1969). Caswell's results suggested that diversity of natural assemblages (including those in the tropics) was maintained in spite of, rather than because of biological interactions between species.

More recently, Tokeshi (1986) used a neutral model to evaluate the temporal organization of nine species of epiphytic Chironomidae in a small river in eastern England and found that real overlap values were far greater than expected by chance alone. He rejected the hypothesis that interspecific competition was influencing the temporal organization of this assemblage and concluded that the abundance of diatoms in the river strongly influenced temporal patterns in assemblage dynamics, especially in terms of production.

So what criteria must be met before a biological assemblage can be considered to be "stable" or "persistent"? Because terminology of assemblage parameters and their usage in the literature vary markedly (see reviews by Harrison 1979, Connell & Sousa 1983), this is not an easy question to answer. Holling (1973) noted that assemblage stability had been interpreted in two ways: (1) as persistence of assemblage structure, and (2) as the degree of constancy in the numbers of organisms over time. Connell & Sousa (1983) followed Holling (1973) by using "persistence" of species to mean their continued presence, particularly in the face of

potentially destructive forces, and they used "stability" to denote relative constancy of numbers over time despite the occurrence of disturbances. On the other hand, constancy of assemblage structure over time was termed "persistence" by Harrison (1979), Grossman (1982) and Lake & Barmuta (1986). Webster *et al.* (1975), Harrison (1979) and Connell & Sousa (1983) all used the term "resistance" to denote the ability of a system to avoid displacement or remain essentially unchanged in size during periods of stress, whereas "resilience" and "inertia" were used to denote this condition by Holling (1973) and Orians (1974), respectively. "Resilience" is now used frequently to infer the ability to recover from an environmental perturbation rather than remain unchanged (Connell & Sousa 1983), Lake & Barmuta 1986). "Determinate" assemblages are viewed as, either those resistant to disturbance, or displaying high resilience following perturbation, characteristics that result in high persistence of assemblage composition over time; the opposite applies to "indeterminate" assemblages (Grossman 1982, Lake & Barmuta 1986).

The effect of stochastic events, especially environmental disturbances on the structure and development of multi-species assemblages is of prime concern to ecologists. Pickett & White (1985) provide an up-to-date account of progress and attitudes in this field. Of particular interest is the Intermediate Disturbance Hypothesis (Connell 1978), which predicts the relative magnitude of biological diversity in a "community" on the basis of the disturbance regime of the physical environment. Where disturbance is intermediate, ie. neither extremely harsh nor benign (however these terms are defined), biological diversity is postulated to be greatest. Species richness of various

marine assemblages appears to conform to this hypothesis (Dayton 1971, Paine 1974, Menge 1976, Connell 1978, Keddy 1983, 1984).

A major problem with the Intermediate Disturbance Hypothesis, lies in the definition of intermediate. In many environments it is almost impossible to define or measure disturbance *per se*, and therefore some correlate of disturbance such as predictability of environmental conditions is measured instead. Truly relevant measures of disturbance must vary depending upon the nature of the environment and the question(s) being asked and both environmental predictability and disturbance intensity need not be immediately apparent. In fact, Yodzis (1978) argued that the effect of intermediate levels of disturbance on species richness was itself dependent on the selectivity of the disturbance and the type of assemblage control. In assemblages controlled by a few dominant species, species richness may increase when disturbance selectively impacts the dominants, whereas species richness may decrease when the disturbance impacts the sub-dominants.

In environments that are frequently (and strongly) disturbed, biological assemblages are predicted to be stochastic with little or no structural persistence as defined by Grossman (1982) and Lake (1986). In contrast, determinate assemblages with marked structural persistence and relatively stable size can be expected to occur in stable environments. These two situations represent the extremes of an environmental continuum along which two habitat characteristics define the position of a particular assemblage: (1) the frequency of disturbance, and (2) the general level of adversity or harshness (Southwood 1988). While straight forward in principle, it is not easy for practising ecologists to place particular assemblages on an environmental gradient since universal scales of harshness remain to be defined.

B. Stream ecology

Until fairly recently, many stream ecologists thought that physico-chemical factors were largely responsible for determining the distribution and abundance of stream organisms (see for example Macan 1963); however, it is now clear that biotic factors can play a role in regulating stream assemblages (see discussions by Hart 1983; McAuliffe 1983, Peckarsky 1983a, 1983b). The relative importance of the two kinds of factors has been considered by Peckarsky (1983a), who concluded that abiotic factors are likely to be of primary importance in physically "harsh" streams, whereas "benign" streams should be more strongly influenced by biotic factors such as predation and competition.

According to Minckley (1963), Bishop (1973), Towns (1976) and Cowie (1980), the most diverse assemblages of benthic stream invertebrates tend to be associated with relatively stable physical environments. In contrast, others (eg. Ward & Stanford 1983) have found a negative correlation between species richness and environmental stability, a finding that implies that strong biotic interactions may reduce species richness in benign stream environments. Although apparently contradictory, these contrasting results reflect the range of environmental conditions considered in the particular studies, and show clearly the difficulties implicit in arriving at useful generalizations.

Effects of fluctuating flows on stream systems have been reported in numerous studies, eg. Gray 1981, Gray & Fisher 1981, Gray & Ward 1982, Fisher & Gray 1983, Dudley *et al.* 1986, McElravy *et al.* (ms), Scrimgeour *et al.* 1988. Floods may result in short- or long-term changes in physical habitats within a stream and may have direct or indirect effects on populations of benthic species. Abundance and biomass of benthic

invertebrates (Siegfried & Knight 1977, Fisher *et al.* 1982, Fisher & Grimm 1987, Rae 1987, Scrimgeour & Winterbourn - in press) and epilithon (Rounick & Gregory 1981, Robinson & Minshall 1986, Scrimgeour & Winterbourn - in press) are usually reduced by floods, but in the long-term, assemblages tend to recover and persist (Molles 1985, Sagar 1986, Srimgeour & Winterbourn in press). In fact, many stream assemblages appear to be extremely resilient (Reice 1984, 1985, Minshall & Petersen 1985, Winterbourn & Rounick 1985, Lake 1986), and although poorly documented, the mobility of assemblage components and existence of nearby sources of colonists (ie. tributaries, backwaters, deeper substrates, riparian zone) appear to contribute substantially to this condition.

If marked physico-chemical fluctuations in the stream environment result in reduced benthic invertebrate densities, assemblage persistence may be strongly dependent on effective recolonization mechanisms: upstream movement of benthic organisms *sensu* Mueller (1974), downstream larval drift, and/or adult dispersal. Since colonization of patches of denuded streambed by invertebrates can be extremely rapid (Townsend 1980, Fisher 1983, Sheldon 1984, Hildrew & Townsend 1987), drift in particular is likely to play a major role in regulating and maintaining the structure of stream assemblages.

Although many stream environments may appear harsh to the observer, members of the stream biota have evolved morphological, behavioural and life history adaptations that reduce physical stresses on them (Hynes 1970, Cummins 1974). Life history patterns, notably the timing of adult emergence and larval recruitment, have important consequences for the persistence of assemblage structure. This is especially true for physically harsh or otherwise extreme lotic environments and a variety of

life history strategies have been described that are appropriate to particular climates and discharge regimes (eg. Resh 1979, Sweeney 1984, Hildrew 1986).

As an environment becomes physically more unstable, denuded habitats occur more frequently and opportunistic or early successional species can be expected to become increasingly important colonizers. Characteristically, they have high reproductive rates, wide physiological tolerances, and as a consequence frequently broad, often cosmopolitan distributions (Grassle & Sanders 1973). The maintenance of relatively high species diversity can depend on their availability and their ability to continually colonize recently disturbed areas of stream (Hildrew 1986).

C. Research objectives

As indicated in this discussion, the nature, persistence and resilience of stream assemblages are strongly influenced by the disturbance regime to which they are exposed. In fact, according to Hildrew & Townsend (1987), stream environments can best be described by two properties: disturbance regimes (or physical processes) and productivity, which is largely determined by water chemistry. In accordance with such thinking, I investigated the role of environmental stability in regulating the dynamics and production of benthic assemblages in four South Westland streams.

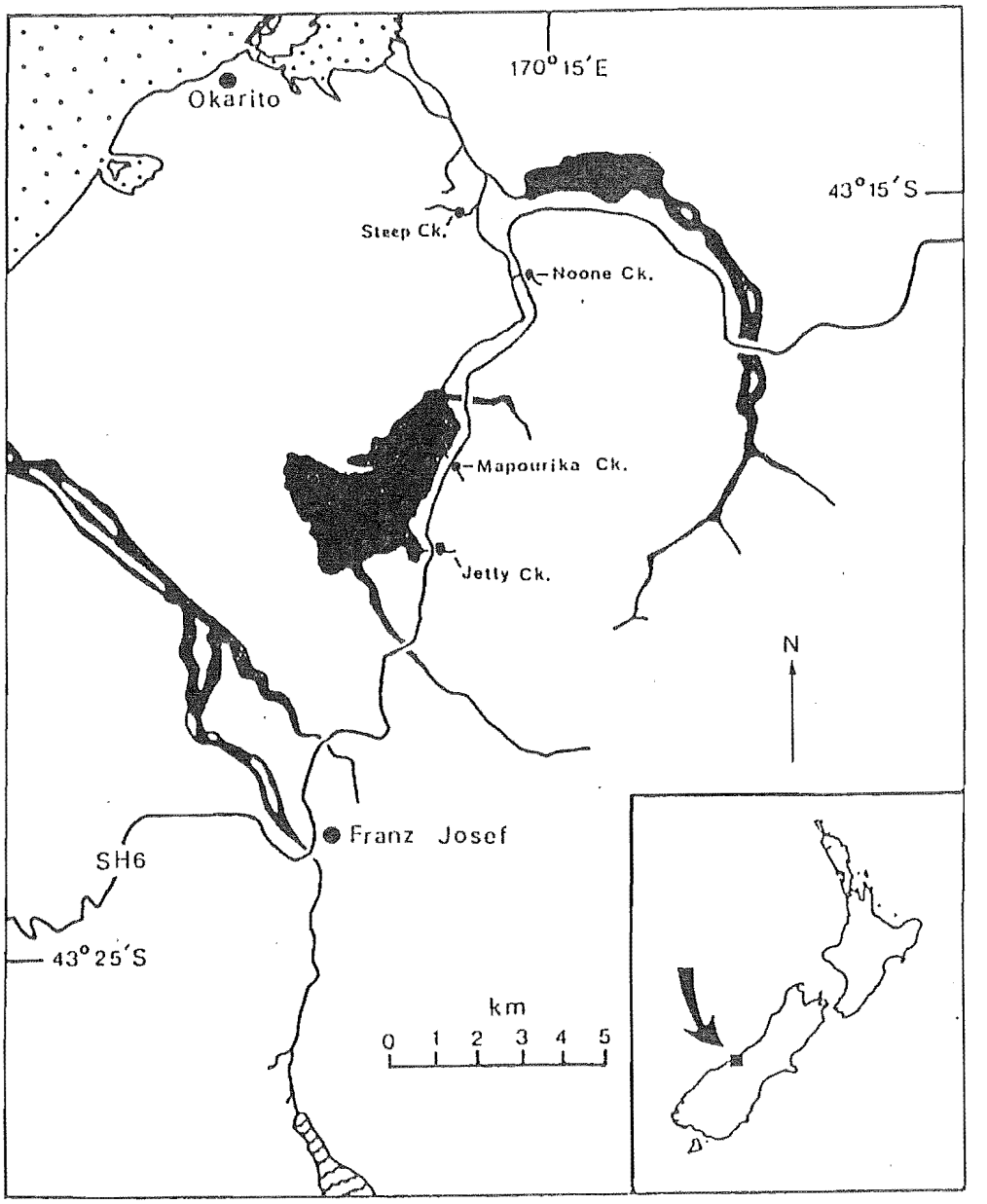



Figure 1.1. Map of the study area showing the locations of sampling sites on the four study streams. The insert shows the location of the study area in the South Island of New Zealand.

Four streams in the Lake Mapourika-Okarito River catchment were monitored intensively, in order to examine the relationship between physico-chemical conditions and benthic "community" structure and productivity. The catchment is in the Waitangi State Forest and Westland National Park on the west coast of the South Island, New Zealand (Fig. 1.1) and the four brownwater streams had similar geology, riparian vegetation and rainfall, but different slopes, discharge, degree of shading and substrate size.

As streams and rivers of the South Westland region generally have markedly fluctuating flow patterns and unstable streambeds as a result of the high and frequent rainfall, the different physico-chemical conditions of the streams might be expected to influence the instream biota in different ways. Specific questions asked were:

1) How do the streams differ in water chemistry in both absolute terms and with respect to temporal variability?
2) Are observed differences related to seasonal and/or physical conditions at the time of sampling?
3) How do epilithic assemblages differ between streams and might differences be related to differences in the physico-chemical environment?
4) Do the streams differ with respect to the retention of organic materials?
5) To what extent do the taxonomic composition, life histories, production and drift of benthic invertebrate assemblages reflect differences in the particular environments of the streams?

# Chapter Two

## STUDY AREA

The four study streams were in the Lake Mapourika - Okarito River catchment, near Franz Josef Glacier on the west coast of the South Island, New Zealand (Fig. 1.1). The sites are described in detail after the climate and local topography of South Westland are outlined briefly. Local climate, particularly during the study period is also described.

### A. South Westland

A long, narrow strip of land lies along the west coast of the south Island between the Main Divide and the Tasman Sea. The northern border of South Westland is the Taramakau River, 16 km south of Greymouth. Westland is divided into two parallel segments by the Alpine Fault, which has caused massive horizontal and vertical displacement of the Earth's crust (Wardle 1979). Vertical uplift formed the steep, outer ranges of the Southern Alps which dominate the region to the east.

As a result of the close proximity of the Southern Alps, stream channels in Westland tend to be steep, short and highly erosive. In many South Westland rivers, suspended sediment yields per annum are ten times greater than average rates for mountainous areas of the world (Griffiths 1979).

Climate of this region is humid and mild, and is characterised by high rainfall that increases from north to south and from the coast towards the mountains. Lowland air temperatures are relatively mild (monthly means range from 6.7 to 15.1 °C), although severe frosts do occur in winter. The number of sunshine hours per annum averages 1840 at

Hokitika (*ca* 100km north of the study area) and maximum daylength is 15 hours in summer and 9 hours in winter.

The nearest climate station to the study area is 20 km further south at the township of Franz Josef Glacier which lies at a similar altitude to the study area. Rainfall there averaged 5236mm per annum from 1976-1986 and was evenly distributed throughout the year (Table 2.1). Rainfalls >0.1mm occur on an average of 177 days per annum and heavy storms can occur at any time. Monthly rainfall totals recorded at Franz Josef Glacier during the study period are also shown in Table 2.1.

**Table 2.1.** Monthly rainfall totals (and their long term means) between January 1976 and December 1986 recorded at the township of Franz Josef Glacier (*ca.* 20 km south of the study area). * indicates years in which study was undertaken.

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1976 | 558 | 112 | 420 | 281 | 407 | 301 | 219 | 218 | 125 | 282 | 233 | 671 |
| 1977 | 561 | 394 | 313 | 385 | 255 | 337 | 157 | 110 | 314 | 350 | 314 | 320 |
| 1978 | 488 | 117 | 563 | 480 | 495 | 166 | 361 | 509 | 582 | 338 | 295 | 380 |
| 1979 | 441 | 369 | 1119 | 614 | 488 | 284 | 385 | 249 | 578 | 554 | 344 | 907 |
| 1980 | 512 | 319 | 321 | 412 | 414 | 290 | 319 | 544 | 849 | 297 | 504 | 311 |
| 1981 | 224 | 522 | 1002 | 475 | 228 | 289 | 409 | 168 | 543 | 486 | 472 | 706 |
| 1982 | 871 | 508 | 837 | 161 | 527 | 147 | 223 | 502 | 326 | 279 | 638 | 387 |
| 1983 | 1002 | 167 | 618 | 598 | 591 | 472 | 450 | 353 | 636 | 764 | 487 | 761 |
| 1984* | 501 | 345 | 619 | 305 | 253 | 427 | 808 | 505 | 355 | 698 | 444 | 1191 |
| 1985* | 707 | 299 | 135 | 428 | 365 | 348 | 392 | 414 | 407 | 188 | 736 | 588 |
| 1986* | 495 | 374 | 369 | 359 | 319 | 629 | 317 | 139 | 252 | 471 | 269 | 485 |
| Mean | 578 | 321 | 574 | 409 | 395 | 335 | 367 | 336 | 452 | 428 | 431 | 609 |

B. Sampling sites

The Lake Mapourika - Okarito River catchment is in the foothills of the Main Divide between the Waiho and Waitangitaona valleys. Its major geographic feature, Lake Mapourika, is a deep body of water lying in an unfilled lobe of an old glacial valley. Its outlet the Okarito River flows north for 10 km before turning northwest to flow into Okarito lagoon and the Tasman Sea.

(i) Stream 1 - Noone Creek

Noone Creek is an unmapped, first order, forested stream that flows into Okarito River about 2 km downstream from the lake. The sampling reach was about 40 m long and 1-2 m wide (Plate 2.1). Streambed slope was gentle (average 1°) and the slope of the surrouding catchment was about 4°. Bed materials are mainly fine sediments (< 2 mm diameter) with some cobbles and pebbles present (Fig. 2.1a). The stream channel was well-defined and contained most "flood" flows.

Riparian vegetation at Noone Creek was mainly rimu (*Dacrydium cupressinum* and kamihi (*Weinmannia racemosa*) with crown fern (*Blechnum discolor*), tutu (*Coriaria arborea*) and tree fern (*Cyathea smithii*) common close to the stream edge. Vegetation formed a canopy, although not a dense one, over the stream channel. Tutu is deciduous, so the canopy was more open in winter than summer. Liverworts were particularly common in the streambed of Noone Creek, and some mosses were also present.

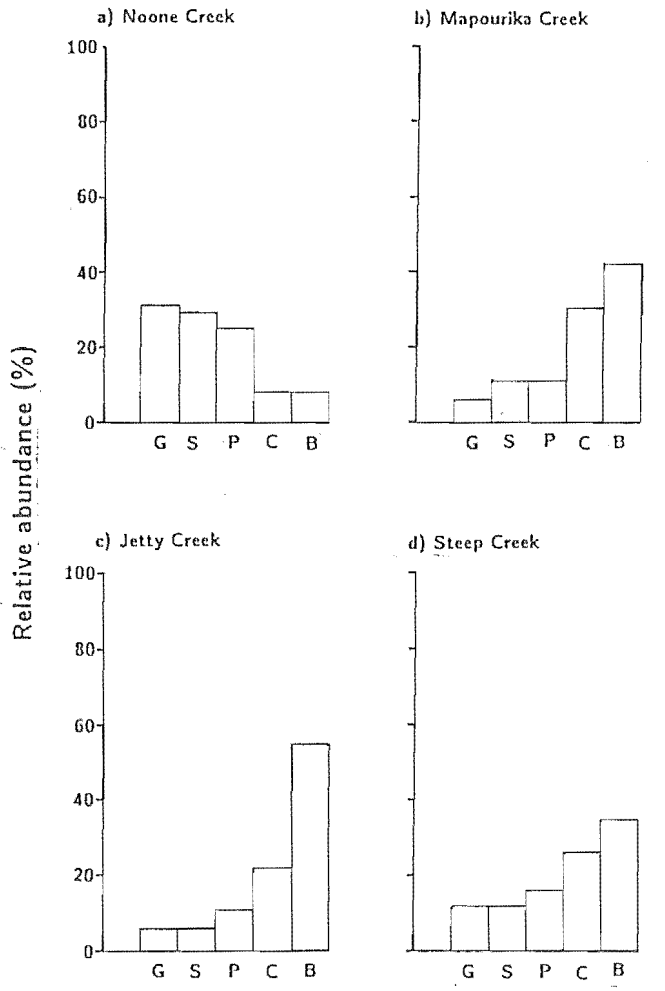



Figure 2.1. Percentage abundance of five grades of sediment (G- gravel, S- sand, P- pebble, C- cobble, B- boulder) in the streambeds of a) Noone, b) Mapourika, c) Jetty and d) Steep Creeks. In May 1986, sediments were mapped along ten transects (one metre apart) across the streambeds. Sediments were classified after Cummins & Lauff (1969).

**Plate 2.1.** Noone Creek, which drains into the Okarito River. Note the gentle slope of the riparian valley and stream channel and abundance of fine sediments in the streambed.

**Plate 2.2.** Mapourika Creek, which drains into Lake Mapourika. Note the dense riparian cover, steep valley and large boulders and cobbles common in the stream channel.

(ii) Stream 2 - Mapourika Creek

Mapourika Creek is a second order stream draining into Lake Mapourika along its eastern shore (Plate 2.2). The section of stream sampled was about 30 m long and 3-8 m wide. Streambed slope averaged 9°, and the slope of the forested valley sides was about 17°. The bed consisted of numerous pools filled with fine sediments and small cascades of moss covered boulders and cobbles (Fig. 2.1b).

Riparian vegetation was similar to that at Noone Creek, except that no tutu was present. Although the vegetation formed a dense canopy over part of the stream channel, much of the sampling reach was exposed to direct sunlight for much of the afternoon. Instream vegetation was mainly mosses growing on boulders and cobbles.

(iii) Stream 3 - Jetty Creek

Jetty Creek is an unmapped, open, first order stream that flows into Lake Mapourika about 2 km south of Mapourika Creek. The sampling reach was about 60 m long and 8-10 m wide (Plate 2.3). Streambed and catchment slopes were highest in this stream (24° and 28°, respectively). In contrast to both Noone and Mapourika Creeks, Jetty Creek had a poorly defined stream channel and water flowed in an ill-defined manner over a series of cascades and between lichen covered boulders and cobbles. The course of the stream within the stream channel changed numerous times during the study period.

Riparian vegetation was similar to that at Noone and Mapourika Creeks, but no riparian canopy was formed. Little instream vegetation was present aside from a few patches of mosses growing in boulder strewn cascades.

**Plate 2.3.** Jetty Creek, which like Mapourika Creek drains into Lake Mapourika. Note the open, steep stream channel and the abundance of large sized sediments in the streambed.

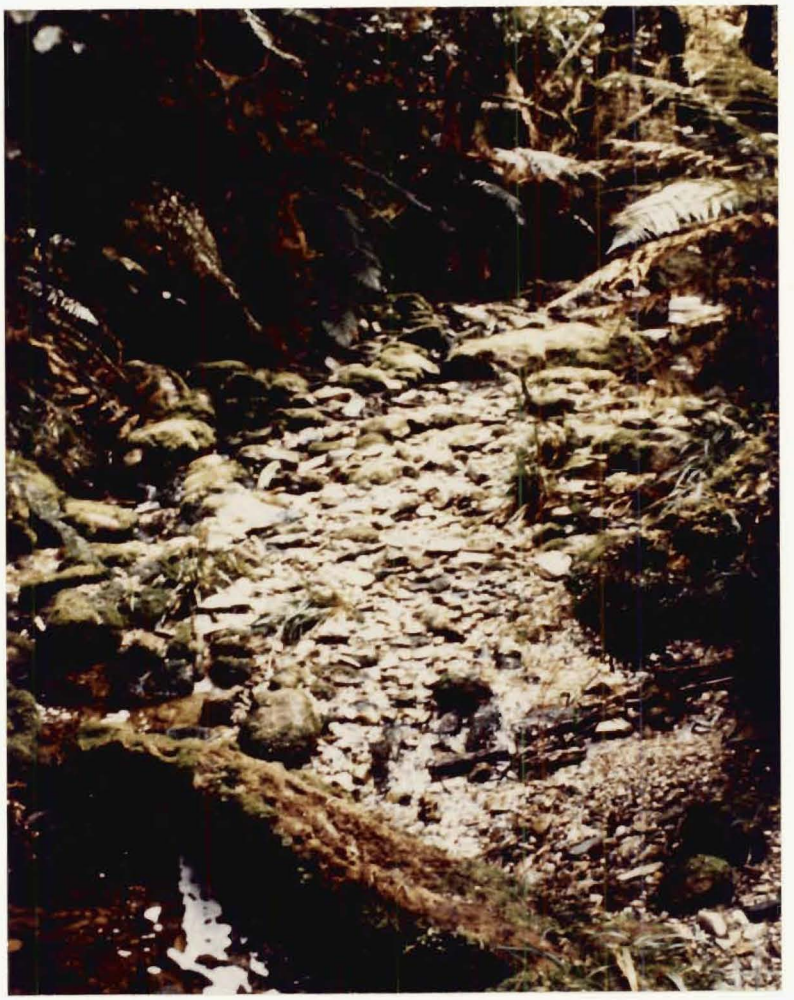


**Plate 2.4.** Steep Creek, which flows into the Okarito River about 2 km downstream from where Noone Creek flows into the river. Note the dense riparian canopy, steep sided valley walls and mixed sediment sizes in the streambed.

(iv) Stream 4 - Steep Creek

Steep Creek is a second order tributary of the Okarito River. Fieldwork was carried out within a 70 m reach where the stream channel was about 3-8 m wide and bed materials were mainly loose and variably embedded cobbles and gravels (Plate 2.4). The streambed was heavily shaded by the steep sided valley walls (slope *ca* 23°) for much of each day. Riparian vegetation was similar to that alongside the other streams. Mosses, liverworts and small patches of the red alga *Batrachospermum* sp. were present in the streambed.

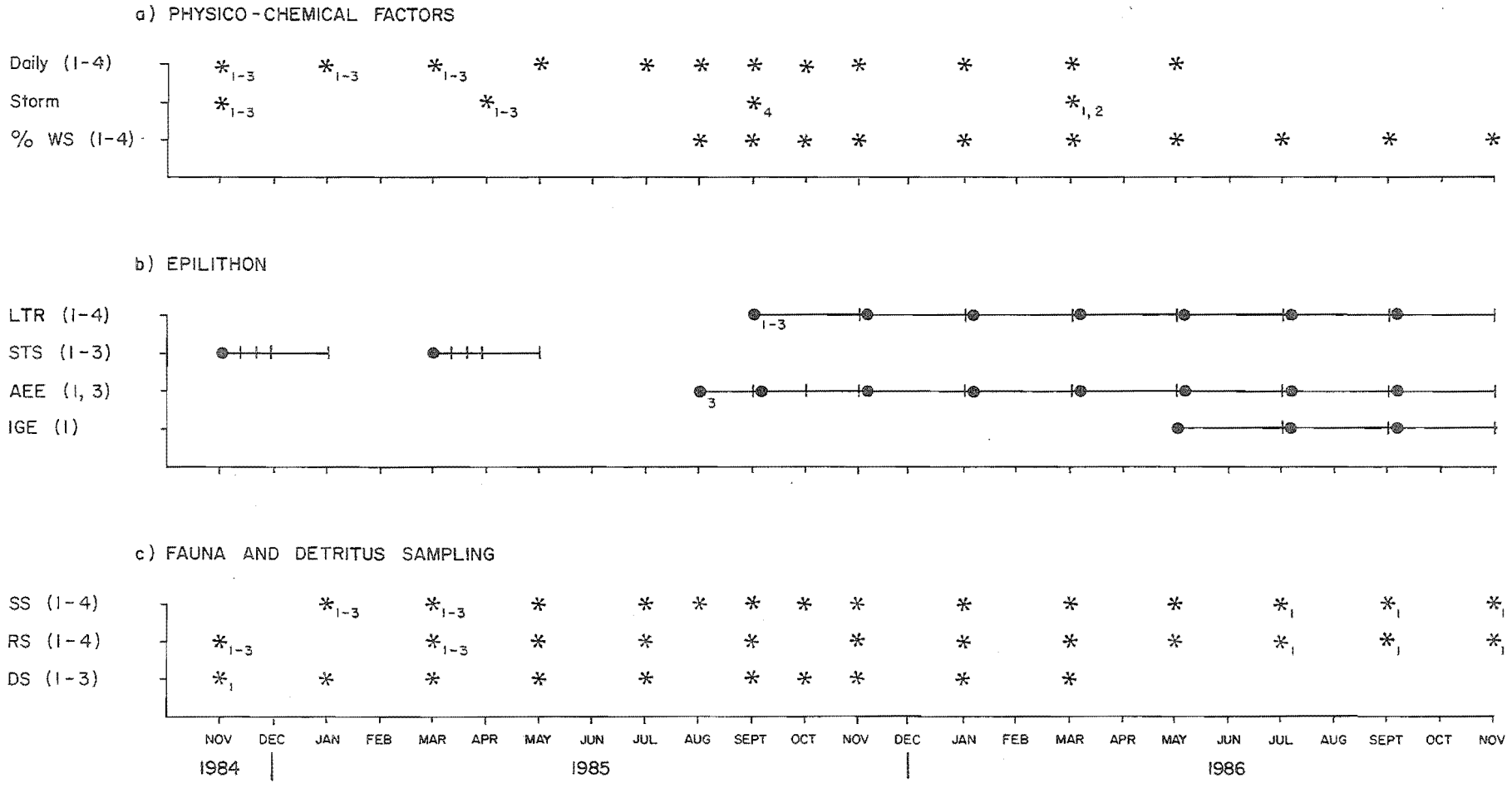
# Chapter Three

## MATERIALS AND METHODS

My field program involved the sampling of selected physico-chemical factors, epilithon, benthic invertebrates, particulate organic matter and invertebrate drift at frequent but irregular intervals. Sampling was carried out on 18 occasions between November 1984 and November 1986 at Noone, Mapourika and Jetty Creeks, however, it began in May 1985 at Steep Creek and was carried out on 11 occasions. Details of the sampling program are shown in Table 3.1.

**Fig. 3.1 (next page):** Summary of field sampling programme for:

(a) physico-chemical factors,
(b) epilithon, &
(c) fauna and detritus sampling
For (a) & (c), * indicates sampling periods
For (b), o, | indicate when artificial substrates were introduced and removed
#'s indicate at which sites sampling occurred
**% WS** - % wet streambed
**LTR** - long-term routine sampling
**STS** - short-term succession sampling
**AEE** - aerial exposive experiments
**IGE** - invertebrate grazing experiment
**SS,RS,DS** - Surber, cobble and drift samples


a) PHYSICO-CHEMICAL FACTORS
Daily (1-4)
Storm
% WS (1-4)
b) EPILITHON
LTR (1-4)
STS (1-3)
AEE (1, 3)
IGE (1)
c) FAUNA AND DETRITUS SAMPLING
SS (1-4)
RS (1-4)
DS (1-3)
NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEPT OCT NOV
1984
1985
1986

A. Physico-chemical measurements

Physical parameters were measured and water samples for chemical analysis collected daily at about 1000 hours during each sampling period. When storm events occurred (see Table 3.1), physico-chemical parameters were measured more frequently as flow conditions changed.

Precipitation was monitored daily at each stream. Rainfall collectors with 15.5 cm diameter plastic funnels similar to those described by McCammon (1978) were placed on the streambank near the sites where discharge measurements were taken. Collectors were calibrated against commercial rain gauges, which showed that 79 ml of water collected was equivalent to 10 mm of rainfall.

Discharge was calculated from measurements of stream width, depth and current speed taken across each stream at a specified site. Measurements were made with a meter rule and a Pygmy Gurley current meter in conjunction with a stopwatch. Depth and current speed were measured at 30 cm intervals across the streams and three estimates of current speed were taken just below the water surface.

Maximum-minimum thermometers held in each stream in protective flow-through plastic tubes were read daily. When water samples were collected, water temperatures were also taken with a hand-held thermometer.

From August 1985 to November 1986 the percentage wetted streambed was estimated during each sampling period to obtain an index of water channel variability. This was done by measuring the amount of channel containing water on ten transect lines crossing the stream within a 20 meter reach at each site.

Water samples (2 litres) were collected in opaque polyethylene bottles. Conductivity and pH were measured within 12 hours of collection using Electrolytic Conductivity Measuring Set Model MC-1 Mark V (Electronic Switchgear Ltd) and Hanna HI 51884 pH stick electrodes, respectively. Conductivity readings were measured and adjusted to equivalent values at 25 °C using the conversion factor given by Golterman (1970). The pH electrode was calibrated daily with pH 4.5 and 7 buffers. Alkalinity was measured within 12 hours by the pH 4.5 titration method described by Mackareth (1963).

Prior to the measurement of dissolved organic carbon concentration (DOC), water was passed through GF/C glass fibre filters (2 um maximum interfibre space) that had been ashed at 350 °C for 6 hours. Both particulate organic carbon (POC -the fraction retained by the filter) and dissolved (DOC) organic carbon concentrations of water samples (500 ml) were measured by the wet oxidation technique described by Collier (1987a,b) for use in New Zealand brownwater streams. This is a modification of the "micro" method described in detail by Maciolek (1962) and Newell (1982).

## B. Instream processing and retention of organic material

### (i) Epilithon on artifical substrates

The structure, biomass and metabolic activity of stone surface biofilms (epilithon) were examined on artifical substrates incubated in the streams for known periods of time between November 1984 and November 1986. Substrates were ornamental tiles (15 $cm^2$) which were held in substrate holders with their unglazed surfaces uppermost. Two types of holder were used.

(a) Flat, single tier substrate holders (Plate 3.1) were used to monitor early colonization and succession of epilithic organisms and to investigate long-term patterns (up to 12 months) in the structure and biomass of epilithon. Colonization and succession was monitored twice over 60 day periods beginning in November 1984 and March 1985. In both series, 40 tiles were placed in each of three streams (Noone, Mapourika and Jetty Creeks) and ten were retrieved after approximately 10, 20, 30 and where possible, 60 days. Following collection, tiles were either fixed for SEM examination (1 tile), used to measure total organic carbon (5 tiles), or assayed for photosynthetic pigments (4 tiles) as described below.

Long-term sampling of the epilithic layers on tiles was carried out routinely between November 1985 and November 1986 at all four streams. Ten tiles were placed in each of the four streams and were removed after approximately two months, except in September and October 1985 when tiles were retrieved from Jetty Creek after 30 days instream incubation only. Following collection, tiles were either fixed for SEM examination (1 tile), used to measure oxygen production, community respiration and total organic carbon (5 tiles), or assayed for photosynthetic pigments (4 tiles) as described below.

(b) Three-tiered substrate holders (Plate 3.2) were placed in Noone and Jetty Creeks, selected because they had most and least variable flow regimes. Tiers were 0, 10 and 20 cm above the substratum and the holders were positioned so that the upper tier was underwater only during the height of flood flows. In contrast, the lowermost substrate was always submerged, and the intermediate one was alternately exposed and covered by water. Between September 1985 and November 1986, seven trials were carried out in Noone Creek and nine trials in Jetty Creek. After

approximately two months colonization, 30 tiles were collected from each stream (10 from each tier). Following collection, they were either fixed for SEM examination (1 tile per tier), used to measure oxygen production, community respiration and TOC (5 tiles per tier), or assayed for photosynthetic pigments (4 tiles per tier) as described below.

One tile collected from each stream on each sampling date was fixed immediately in 3% gluteraldehyde in phosphate buffer. Later, tiles were rinsed twice with clean phosphate buffer and taken through an ethanol series (30, 50, 70, 80, 90 and 100% twice). Tiles were kept overnight in the second 100% ethanol solution, air dried and coated with 16nm of gold prior to viewing with a Cambridge Stereoscan S250 Mk II scanning electron microscope (SEM) at an accelerating voltage of 20 kV. Photographs were taken at various magnifications to provide a permanent record of epilithic organisms and assemblage structure.

Oxygen production and respiration of stone surface communities were measured by incubating tiles in sealed 50 ml glass jars of still streamwater at ambient streamwater temperature (±2°C) in the light for 12 hours and then in total darkness for 12 hours. The light source used was a 20 Watt Atlas artificialdaylight tube placed above the jars at a distance of 23 cm. After both the light and dark incubation periods, oxygen concentrations were measured with a YSI model 54 oxygen meter and electrode. Respiration and net photosynthetic rates were calculated as mg $O_2$ used or produced per $cm^2$ of tile surface per hour. Five control jars were run concurrently with the experimental jars and contained streamwater with a clean (ie. uncolonized) tile.

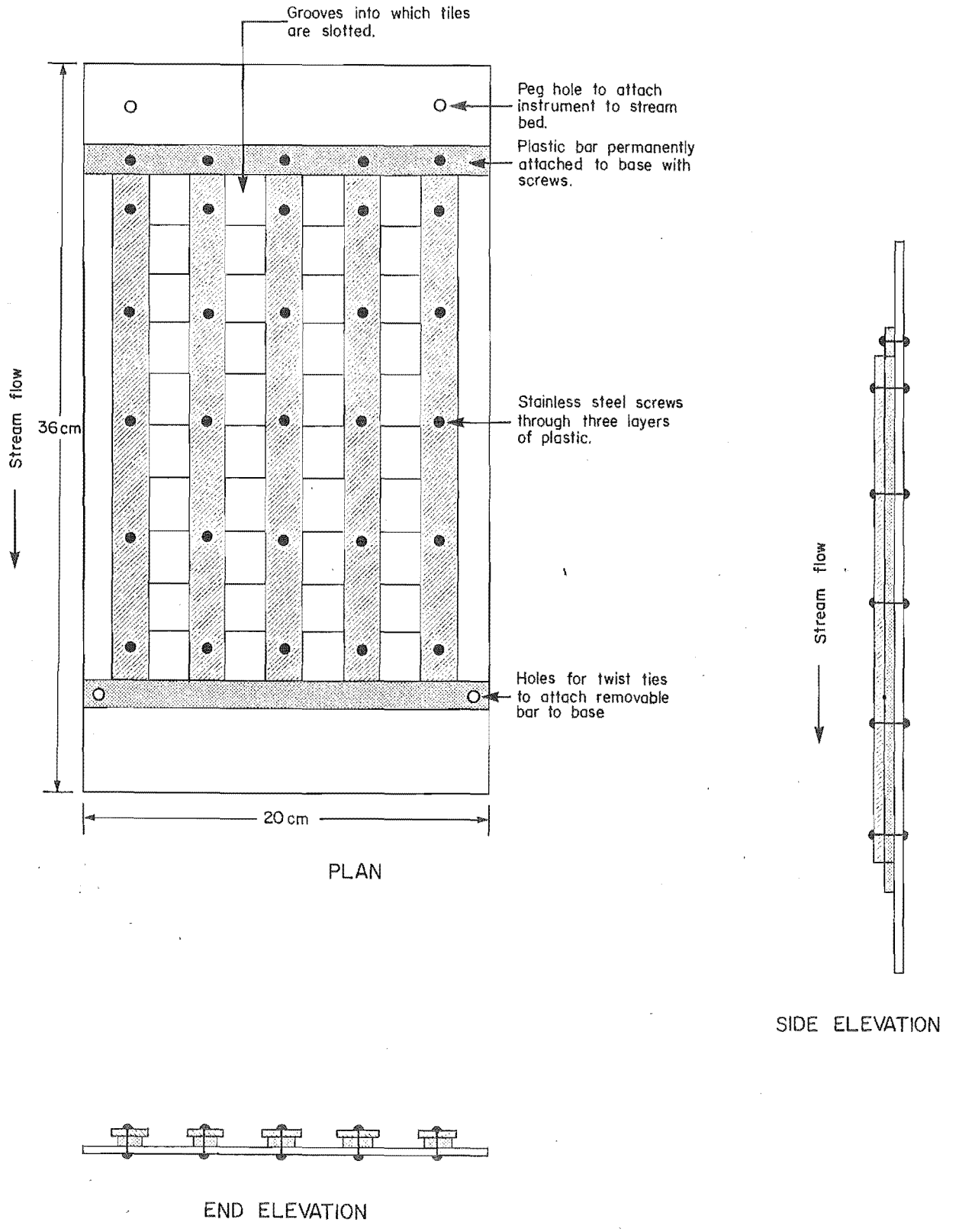



Figure 3.2. Diagram showing the dimensions and construction of the single-tiered tile holder. Forty tiles are held in one of the four tracks (ie. ten tiles in each track). Holders were attached securely to the streambeds of Mapourika and Steep Creeks by long stainless steel pegs.

Organic carbon content of epilithon on tiles was determined with the "semi micro" dichromate oxidation method of Maciolek (1962) but 1N rather than 2N potassium dichromate solution was used as recommended by Cowie (1980). Total organic carbon was expressed as micrograms per $cm^2$.

Photosynthetic pigments were extracted from epilithon on tiles with 90% acetone to which a small quantity of $MgCO_3$ was added. The extraction procedure was carried out at 4 °C in the dark for 24 hours. Extract absorbances were read at 410, 430, 665 and 720 nm on a Pye Unicam SP 1800 spectrophotometer and pigment concentrations (chlorophyll *a* and phaeophytin *a*) were calculated by the method of Moss (1967 a,b). Concentrations of chlorophyll *a*, phaeophytin *a* and total pigment (ie. chlorophyll plus phaeophytin) were recorded as micrograms of pigment per $cm^2$ of exposed tile surface. Percent phaeophytin concentrations were calculated using the 430:410 absorbance ratio graphical procedure and a standard curve based on average values for algal communities given by Moss (1967a).

(ii) Effect of invertebrate grazing on epilithon

Twelve red brick tiles (20x 10x 1.5 cm) smooth on one face and with five longitudinal furrows on the other were placed furrow side up in Noone Creek in May, July and September 1986 to investigate the effect of grazing by invertebrates on epilithon biomass accumulation. "Petroleum jelly barriers" similar to those described by McAuliffe (1984) were used to exclude invertebrate grazers from six of the tiles, while the other six in each series lacked barriers. After 2 months, tiles were removed from the stream and total organic carbon content on three "grazed" and three "ungrazed" tiles was measured by the "semi-micro", wet oxidation technique.

(iii) Detritus stored within the streambed

Detritus stored within the beds of all four streams was collected with a Surber sampler (0.1 $m^2$, 0.25 mm nylon mesh net) in samples used to obtain benthic invertebrates (5 samples per stream per sampling occasion). After removing invertebrates from alcohol-preserved sample, the remaining material was dried at 60 °C for at least 5 days, weighed, ashed at 600 °C for 6 hours and re-weighed. The final weight, ie. the inorganic component, was subtracted from the initial dry weight of the sample to estimate the ash free dry weight (AFDW) of detritus. Detritus therefore represented all non-animal organic material trapped by the 0.25 mm mesh net.

The amount of detritus present in other quantitative faunal collections (ie. cobble and drift samples, see below) was also measured and expressed in appropriate units.

C. Faunal sampling

Quantitative sampling of benthic invertebrates was carried out in all four streams with a Surber sampler (0.1 $m^2$; 0.25mm mesh net) between November 1984 and May 1986 and was continued at Noone Creek until November 1986. Sediments enclosed by the sampler frame were tumbled by hand to dislodge and remove all animals, plant material and accumulated debris. Sediments were often highly compacted and it was difficult to disturb them to a depth greater than 10 cm. Five samples were taken from the same section of each stream on all occasions. Current speed and depth of water were measured immediately upstream of the sampler.

In addition to Surber samples, invertebrates were collected from 5 individual cobbles (20-50 cm diameter) using a hand net (0.25 mm nylon mesh) placed behind the cobble, which was quickly lifted into the net. The cobble surface was scrubbed to remove all animals and attached plant material. Before the cobble was sampled, current speed (Pygmy Gurley meter) and depth were measured in front of the cobble. In the laboratory, the surface area of each cobble was measured using the plastic film technique described by Doeg & Lake (1981).

Drifting invertebrates were sampled at Noone, Mapourika and Jetty Creek at approximately 2-monthly intervals on 10 occasions between November 1984 and March 1986. Sampling was undertaken simultaneously at the 3 streams with nets being emptied before sunset and after sunrise on 2 consecutive days. Drift nets (0.25 mm mesh; 1.2 m long; 7 x 25 cm mouth; 1 net per stream) were placed in areas of rapid flow with the entire net opening just below the water surface and above the substratum. Current speed and depth were measured when nets were emptied so that an estimate of the volume of water that had flowed through the net could be obtained.

General collections of invertebrates were made with a kick net (0.25 mm mesh) in a variety of habitats including backwaters, leaf packs and overhanging riparian vegetation to obtain additional animals for life history studies. Five "sticky" traps (boards coated with a mixture of polybutene, epolene N10 wax and tacifying resin in a ratio of 10:3:1.5) were set out along each stream to catch emerging stream insects.

All faunal samples were preserved in the field with 70% alcohol and animals were sorted, identified and counted at 40x magnification using an Olympus binocular dissecting microscope. Identification was to the generic and where possible specific level (except for Chironomidae) using

the keys of Cowley (1978) - general Trichoptera, McFarlane (1951) - Hydrobiosidae, Towns (1983a), Towns & Peters (1979) - Ephemeroptera, and Winterbourn & Gregson (1981) - other aquatic taxa.

Body sizes of selected invertebrate taxa belonging to three orders of insects (Ephemeroptera, Plecoptera and Trichoptera) collected in benthic samples, were measured to obtain information on life histories (Surber, cobble and kick samples) and secondary production (Surber samples only). Maximum distance across the head capsule of each specimen (Head Capsule Width or HCW) was used as an index of animal body size and was measured with a calibrated eyepiece micrometer to the nearest 0.16 mm.

(i) Additional fieldwork

Additional fieldwork was undertaken to examine -

(a) preference of invertebrate grazers for "grazed" and "ungrazed" epilithon, and

(b) effect of substrate size on invertebrate colonization.

These two experiments formed a minor component of the study; and the protocol followed for each experiment and the obtained results are presented and interpreted in Appendix Three. Where appropriate, results are discussed with the other findings of the study.

# Chapter Four

## PHYSICO-CHEMICAL CONDITIONS

### A. Long term sampling program

Selected physical and chemical parameters were monitored in three streams (Noone, Mapourika and Jetty Creeks) on 12 occasions between November 1984 and July 1986. Steep Creek was sampled in a similar fashion 9 times between May 1985 and July 1986. Sampling was generally carried out over 3-5 day periods except in November-December 1984, when it was continued for 25 days. The physical factors measured were discharge, percentage wet streambed and temperature, and the chemical parameters were pH, conductivity, alkalinity and dissolved organic carbon (DOC). Particulate organic carbon (POC - >0.45 um) in suspension was also monitored.

#### (i) Noone Creek

a) Physical factors (Fig. 4.1 a-c)

Mean daily discharges during the 14 sampling periods ranged from 4 to 47 $l.s^{-1}$ and no seasonal patterns were evident. Maximum discharge recorded for a single day was 330 $l.s^{-1}$ on 17 December 1984 after 101 mm of rain fell overnight. Daily discharge was correlated significantly with the rainfall recorded in the previous 24 hours (Table 4.1).

Percentage wet streambed was positively correlated with the daily discharge recorded on the day of sampling (Table 4.2) and ranged from 60 to 87 percent (coefficient of variation= 12%, n= 10). Like discharge, no seasonal patterns in percentage wet streambed were found.

Table 4.1. Spearman rank correlation coefficients between daily discharge and rainfall recorded at each stream in the preceding 24 hours; n= number of sampling periods.

| Streams | $r_s$ | p | n |
|---|---|---|---|
| Noone Creek | 0.567 | p< 0.05 | 13 |
| Mapourika Creek | 0.536 | p< 0.05 | 13 |
| Jetty Creek | 0.637 | p< 0.05 | 11 |
| Steep Creek | 0.714 | p< 0.05 | 8 |

Table 4.2. Spearman rank correlation coefficients between percentage wet streambed and discharge recorded at the 4 streams between August 1985 and November 1986; n= number of sampling periods.

| Streams | $r_s$ | p | n |
|---|---|---|---|
| Noone Creek | 0.714 | p< 0.05 | 10 |
| Mapourika Creek | 0.731 | p< 0.05 | 10 |
| Jetty Creek | 0.902 | p< 0.01 | 10 |
| Steep Creek | 0.800 | p< 0.01 | 10 |

Water temperatures ranged from 5 to 19 °C with minima in July, August and September and maxima between December and March. During periods of heavy rainfall, daily water temperature ranges were narrow (eg. 15 March 1986, 14-15 °C), but when discharge was low (eg. 14 March 1986), temperature ranges were wider (12-17 °C).

b) Chemical parameters and organic carbon content of water (Fig. 4.2 a-e)

Streamwater pH ranged from 5.3 to 6.0, conductivity from 18 to 31 $uS.cm^{-1}$ and alkalinity from 2.2 to 8.9 mg $CaCO_3.l^{-1}$. All these parameters were highest in April 1985. DOC content of stream water ranged from 3.9 to 10.5 $mg.l^{-1}$ and POC ranged from 0.6 to 3.0 $mg.l^{-1}$. No seasonal trends were shown by the water chemistry parameters measured.

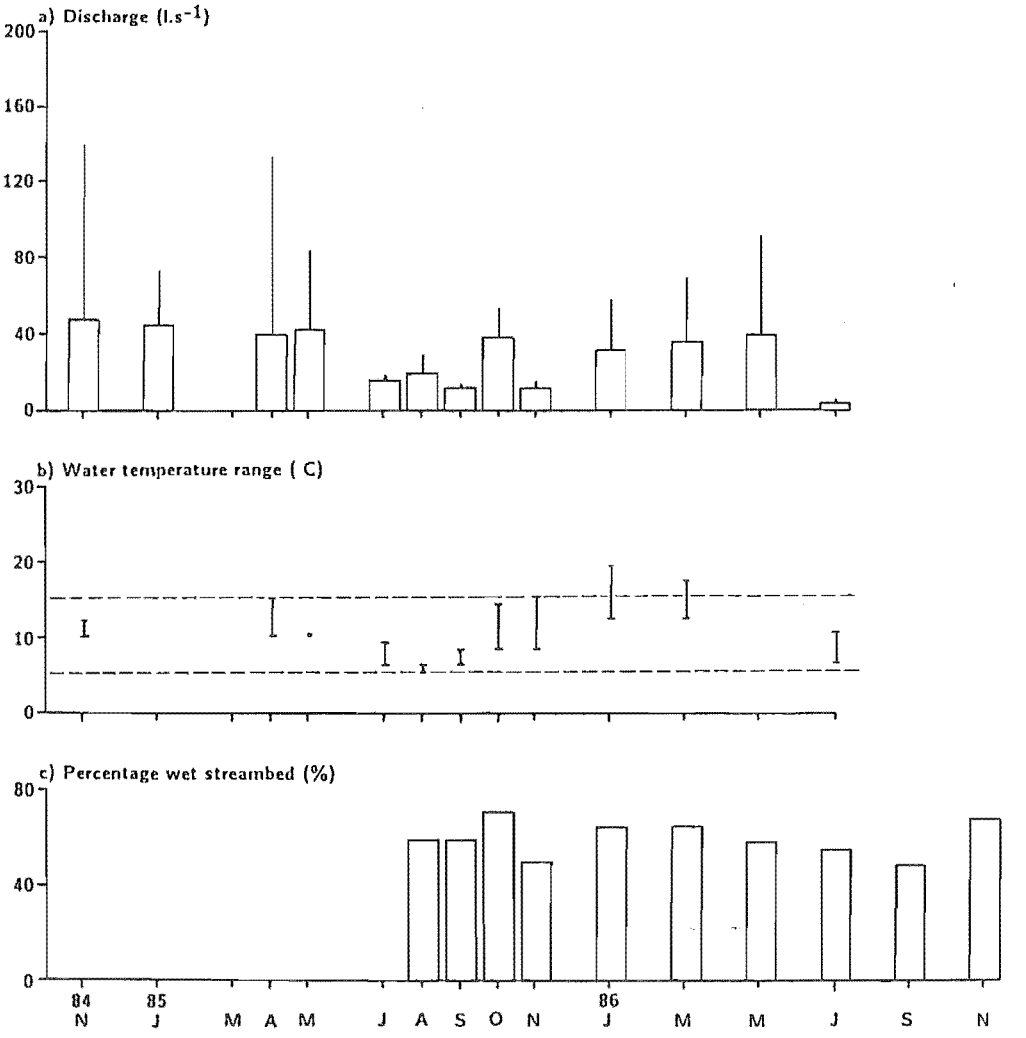



**Figure 4.1.** Summary of physical parameters measured at Noone Creek during 3-5 day sampling periods (25 days in November 1984) between November 1984 and November 1986 - a) mean daily discharge (±2SE), b) maximum and minimum water temperatures, c) percentage wet streambed. Labelling for all X-axes indicated on c).

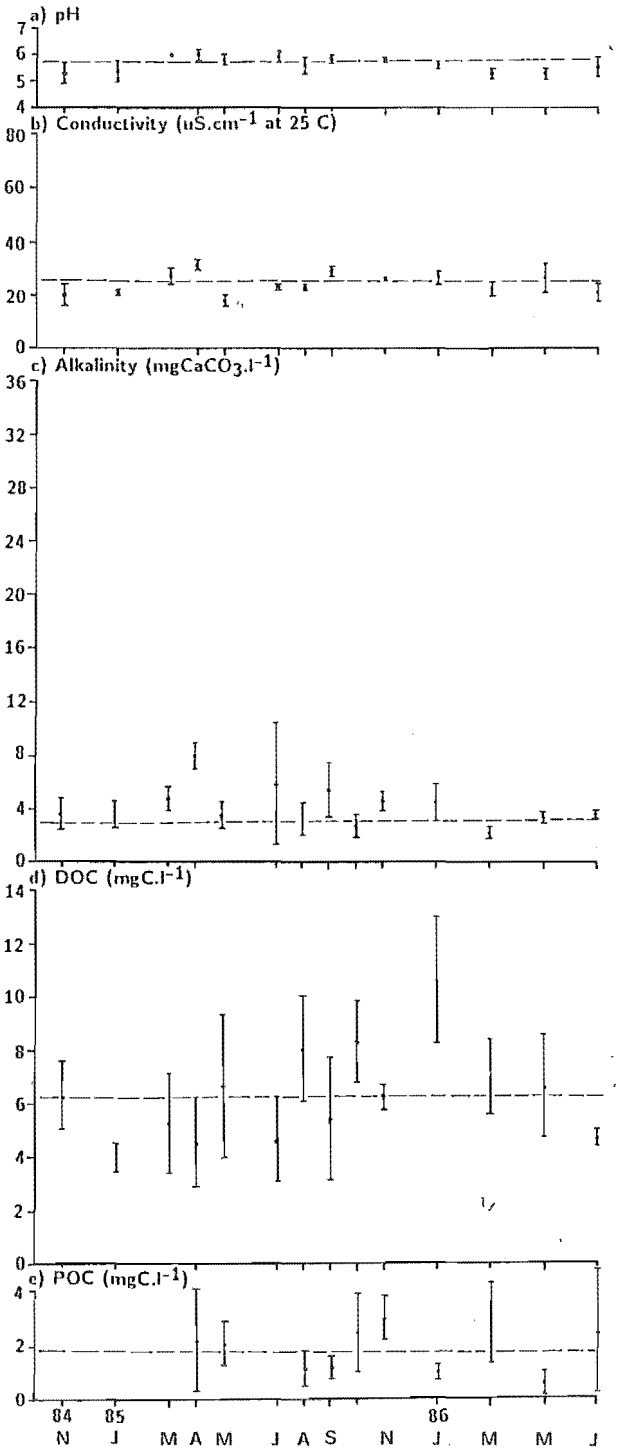



Figure 4.2. Summary of water chemistry parameters measured at Noone Creek during 3-5 day sampling periods (25 days in November 1984) between November 1984 and July 1986. Daily means (±2SE) are given for a) pH, b) conductivity, c) alkalinity, d) dissolved organic carbon concentration (DOC), e) particulate organic carbon concentration (POC). Dashed lines indicate overall mean values. Labelling for all X-axes indicated on e).

(ii) Mapourika Creek

a) Physical factors (Fig. 4.3 a-c)

Mean daily discharge during the 14 sampling periods ranged from 24 to 149 $l.s^{-1}$ and as in Noone Creek, no seasonal patterns were apparent. The highest discharge on a single day was 900 $l.s^{-1}$, recorded on 17 December 1984. Discharge and rainfall at the stream site during the preceding 24 hours were significantly correlated (Table 4.1).

The proportion of streambed covered in water ranged from 35 to 62 percent and was both lower and more variable (CV= 18%) than at Noone Creek. As at Noone Creek, this measure was positively correlated with discharge recorded at the time of sampling (Table 4.2).

Water temperature ranged from 5 to 23 °C and summer maxima were up to 6 °C greater than at Noone Creek. This can be attributed to the more open, westerly aspect of the streamsite which faces Lake Mapourika. Daily temperature ranges were lower during high flows (eg. 5-19 December 1984, 10-14 °C) than during low flow periods (ie. 1-4 December 1984, 9-20 °C).

b) Chemical parameters and organic carbon content of water (Fig. 4.4 a-e)

Streamwater pH ranged from 4.8 to 6.5, conductivity from 17 to 67 $uS.cm^{-1}$ and alkalinity from 4.6 to 28.3 mg $CaCO_3.l^{-1}$. DOC and POC concentrations ranged from 2.3 to 5.6 $mg.l^{-1}$ and 0.8 to 2.6 $mg.l^{-1}$, respectively. As at Noone Creek, no seasonal patterns were apparent.

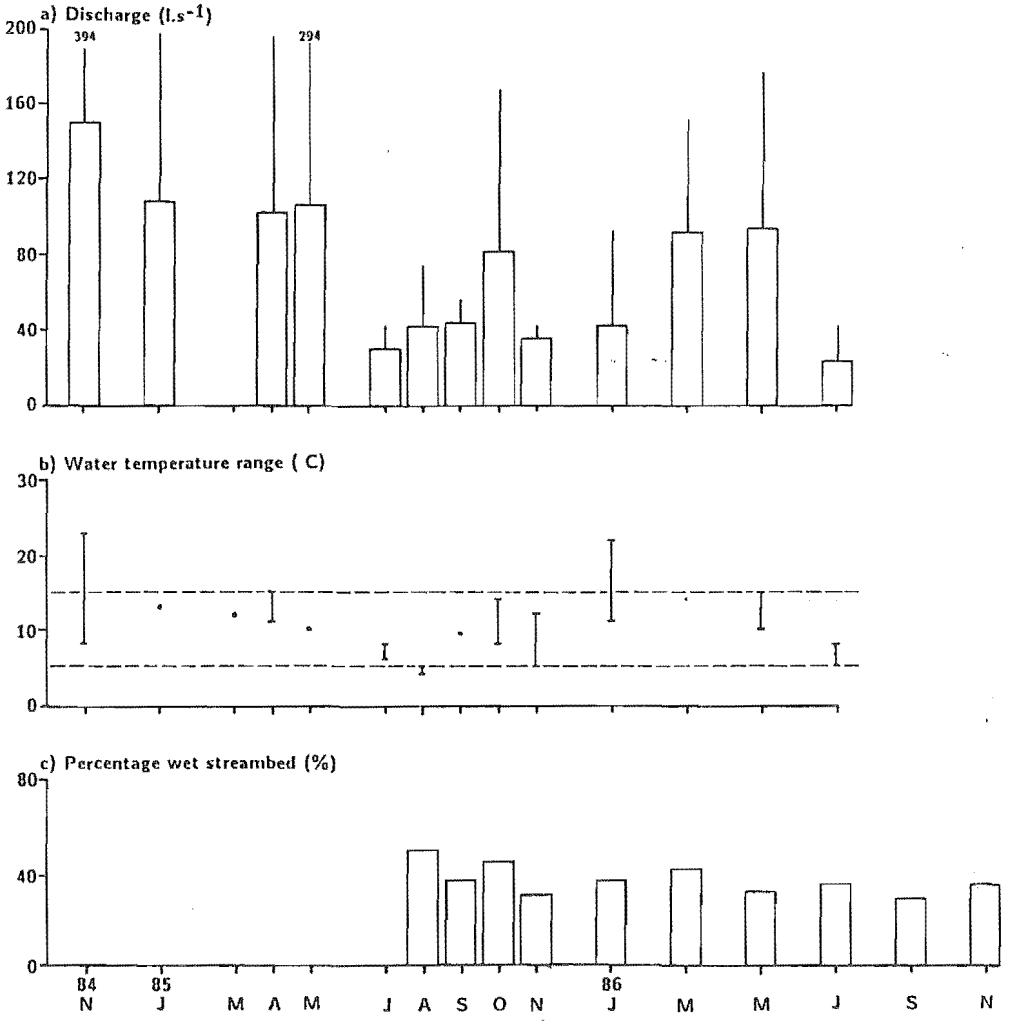



Figure 4.3. Summary of physical parameters measured at Mapourika Creek during 3-5 day sampling periods (25 days in November 1984) between November 1984 and November 1986 - a) mean daily discharge (±2SE), b) maximum and minimum water temperatures, c) percentage wet streambed. Labelling for all X-axes indicated on c).

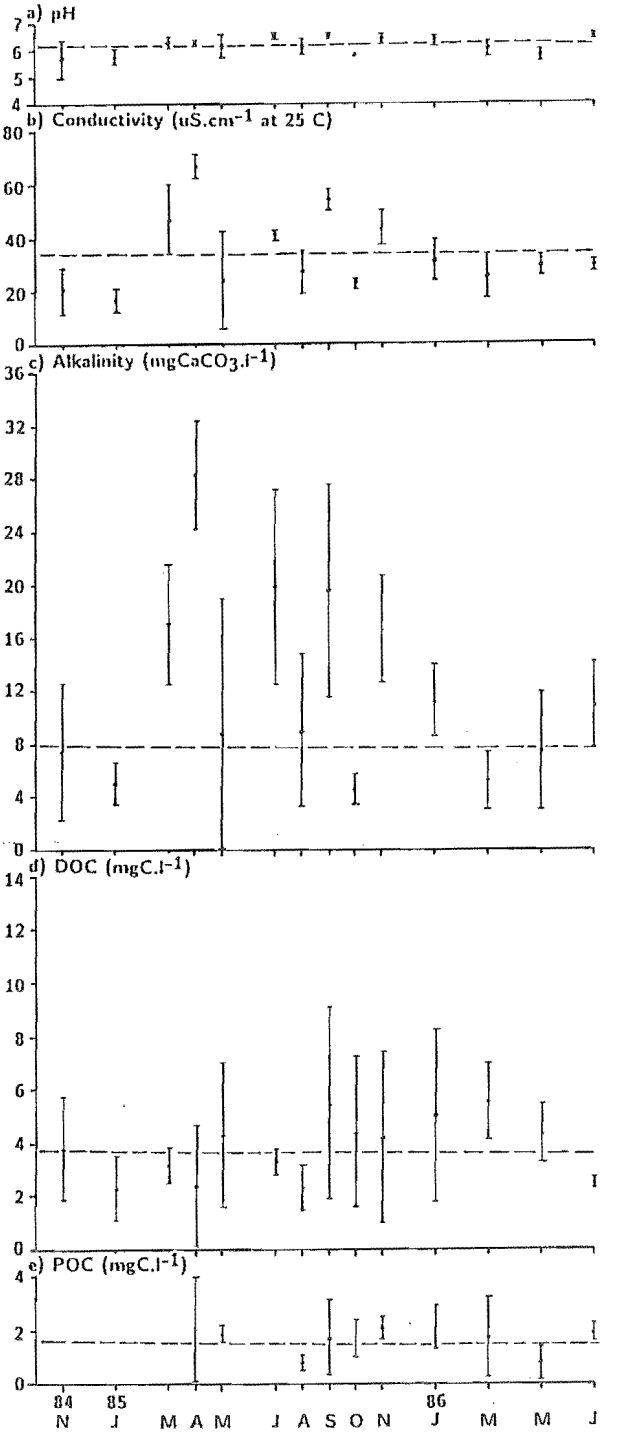



Figure 4.4. Summary of water chemistry parameters measured at Mapourika Creek during 3-5 day sampling periods (25 days in November 1984) between November 1984 and July 1986. Daily means (±2SE) are given for a) pH, b) conductivity, c) alkalinity, d) DOC, e) POC. Dashed lines indicate overall mean values. Labelling for all X-axes indicated on e).

(iii) Jetty Creek

a) Physical factors (Fig. 4.5 a-c)

Mean daily discharge during the 14 sampling periods ranged from 0.25 to 93 $l.s^{-1}$ and the highest discharge recorded on a single day was 660 $l.s^{-1}$ on 30 November 1984. Discharge minima thus were lower than in Noone and Mapourika Creeks but maxima were of intermediate intensity. Again, no seasonal trends in stream discharge were evident and discharge was significantly correlated with rainfall in the previous 24 hours (Table 4.1).

Percentage wet streambed ranged from 10 to 40 percent and therefore was substantially lower and more variable (CV= 37%, n= 10) than at Noone and Mapourika Creeks. Once again, percentage wet streambed was strongly correlated with discharge at the time of sampling (Table 4.2) and no seasonal patterns were apparent.

The range of water temperatures recorded was identical to that found in Mapourika Creek (5-23 °C, Fig. 4.5c). Jetty Creek also faces Lake Mapourika and receives uninterrupted afternoon sun. During spates, water temperatures decreased and daily temperature ranges were reduced (eg. 5-19 December 1984, 10-14 °C).

b) Chemical parameters and organic carbon content of water (Fig. 4.6 a-e)

Streamwater pH was always lower than in Noone and Mapourika Creeks and ranged from 4.5 to 5.0. Conductivity was also lower than in the other streams (14-25 $uS.cm^{-1}$) and alkalinity was always low (1.3-3.0 mg $CaCO_3.l^{-1}$). DOC concentrations ranged from 2.1 to 7.9 $mg.l^{-1}$, whereas POC concentrations were always low (0.3-2.0 $mg.l^{-1}$). Again, no seasonal trends were observed.

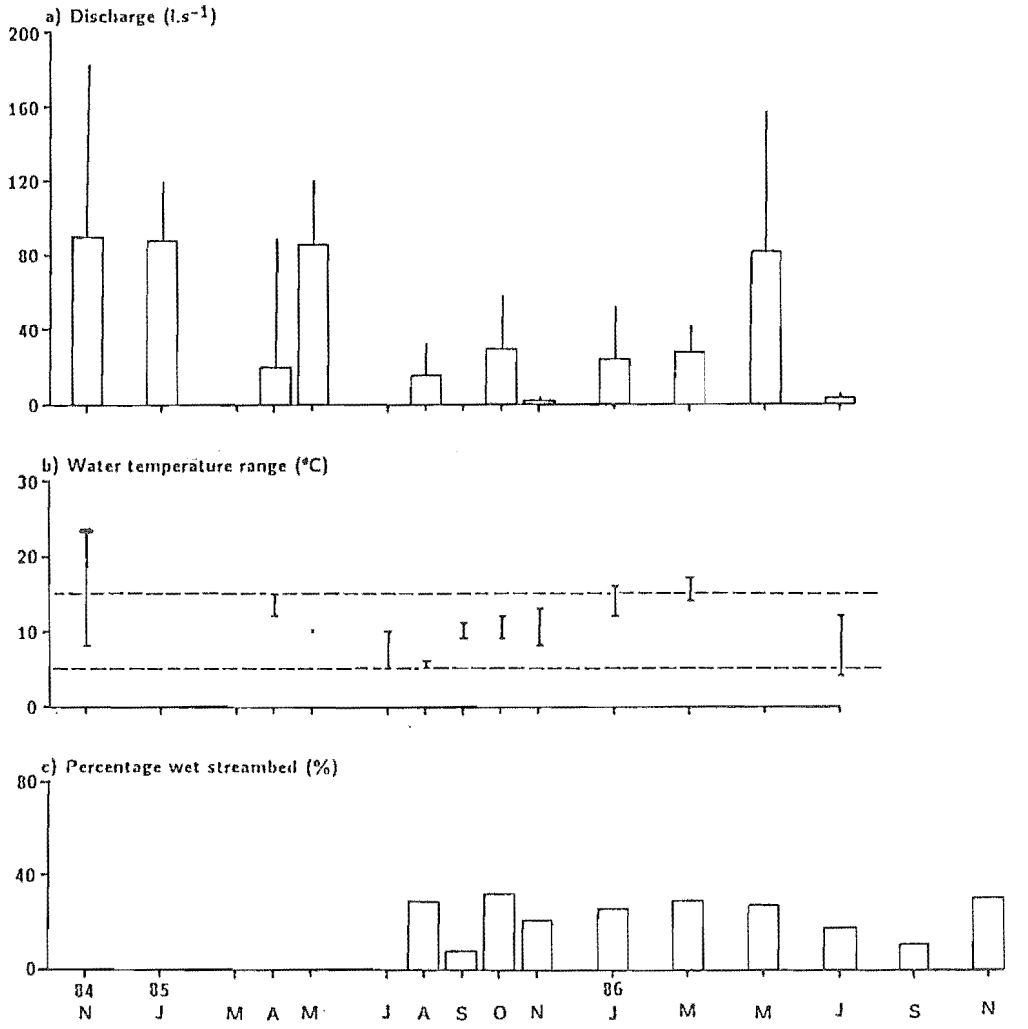



Figure 4.5. Summary of physical parameters measured at Jetty Creek during 3-5 day sampling periods (25 days in November 1984) between November 1984 and July 1986 - a) mean daily discharge (±2SE), b) maximum and minimum water temperatures, c) percentage wet streambed. Labelling for all X-axes indicated on c).

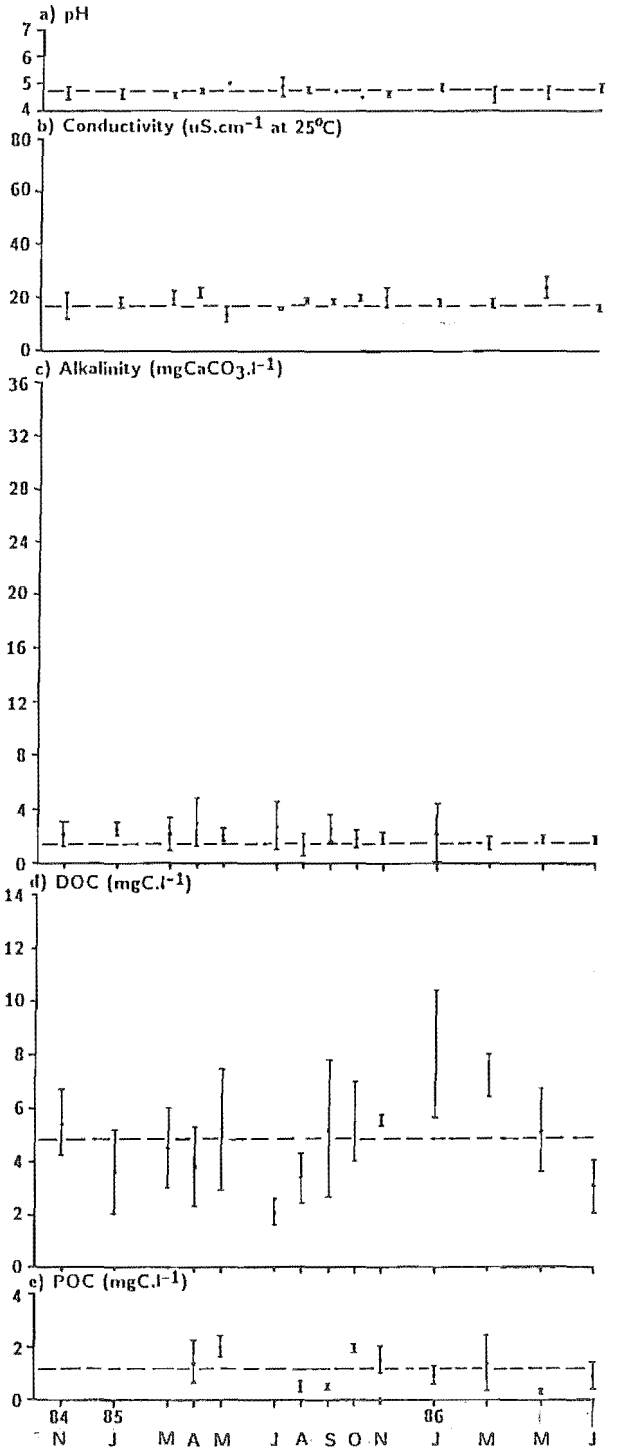



Figure 4.6. Summary of water chemistry parameters measured at Jetty Creek during 3-5 day sampling periods (25 days in November 1984) between November 1984 and July 1986. Daily means (±2SE) are given for a) pH, b) conductivity, c) alkalinity, d) DOC, e) POC. Dashed lines indicate overall mean values. Labelling for all X-axes indicated on e).

(iv) Steep Creek

a) Physical factors (Fig. 4.7 a-c)

Monitoring of Steep Creek began in May 1985 and was continued until July 1986. Records therefore are less extensive than for the other 3 sites.

Daily discharges recorded during the 9 sampling periods ranged from 2 to 332 $l.s^{-1}$ and were significantly correlated with rainfall recorded within the previous 24 hours (Table 4.1). The highest discharge recorded on a single day was 886 $l.s^{-1}$ on 4 September 1985 after 123 mm of rain had fallen overnight at the stream site. No seasonal patterns were apparent.

Percentage wet streambed varied from 32 to 66 percent and was more variable than in all the other streams (CV= 26%, n= 10). Percentage wet streambed was positively correlated with discharge (Table 4.2).

The annual water temperature range at Steep Creek was 5 to 17 °C, the lowest range of the 4 streams. The low summer maximum reflects the extremely shaded nature of the stream which flows through a very steep-sided valley that prevents sunlight from penetrating to the stream bed during most of the day.

b) Chemical parameters and organic carbon content of water (Fig. 4.8 a-e)

Streamwater pH was similar to that of Jetty Creek and averaged about 4.6 (range 4.2-5.2). Conductivity ranged from 20 to 33 $uS.cm^{-1}$ and alkalinity was always between 1.2 and 2.5 mg $CaCO_3.l^{-1}$. DOC and POC concentrations were similar to those recorded in Noone Creek (4.6-10.4 and 0.7-3.8 $mg.l^{-1}$, respectively).

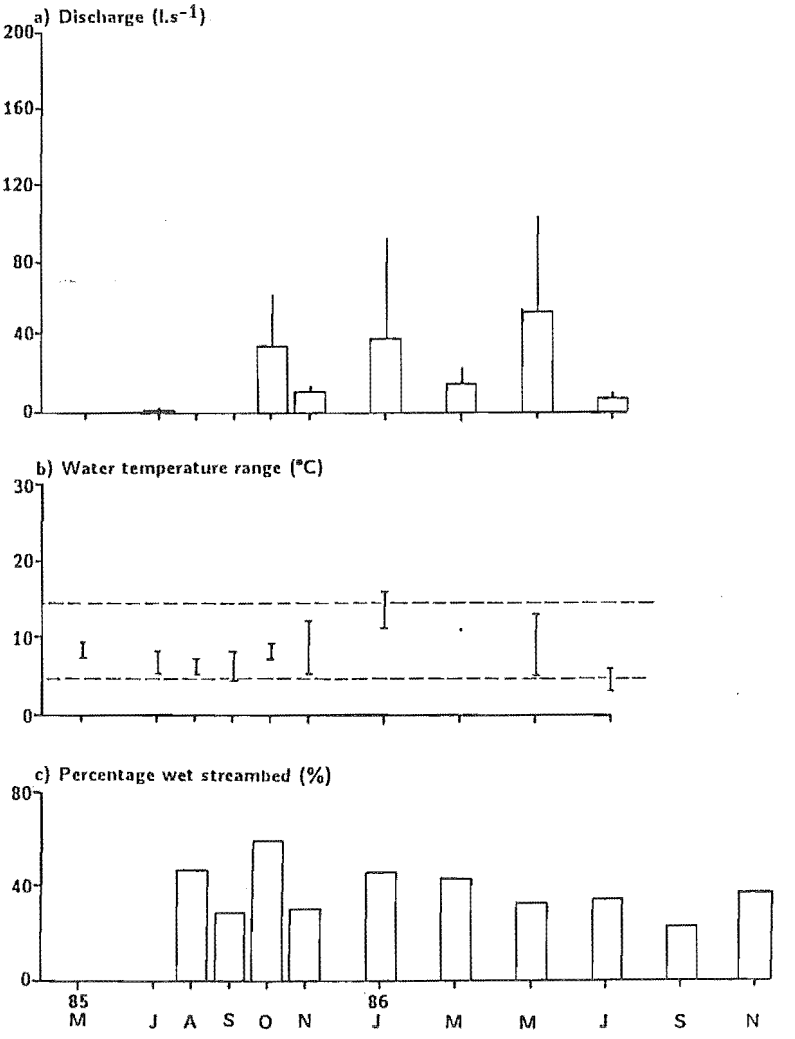



Figure 4.7. Summary of physical parameters measured at Steep Creek during 3-5 day sampling periods between May 1985 and November 1986 - a) mean daily discharge (±2SE), b) maximum and minimum water temperatures, c) percentage wet streambed. Labelling for all X-axes indicated on c).

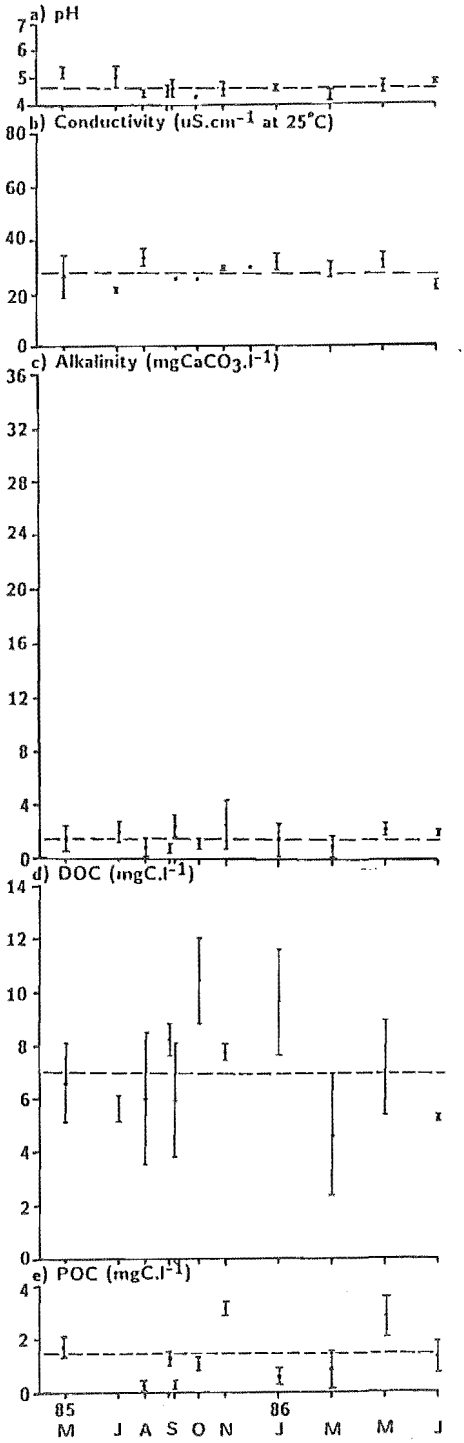



Figure 4.8. Summary of water chemistry parameters measured at Steep Creek during 3-5 day sampling periods between May 1985 and July 1986. Daily means (±2SE) are given for a) pH, b) conductivity, c) alkalinity, d) DOC, e) POC. Dashed lines indicate overall mean values. Labelling for all X-axes indicated on e).

(v) Comparisons among streams (Tables 4.3, 4.4)

Mean daily discharges were significantly different among the streams, and reflect differences in the sizes of their catchments. Highest streamflows were recorded in Mapourika Creek, which drained the largest catchment, and lowest flows were observed in Jetty Creek, which drained the smallest catchment. No seasonal patterns in discharge were apparent, but discharge was positively correlated with rainfall recorded at each stream.

**Table 4.3.** Results of Friedman's two-way non-parametric ANOVA carried out on selected physico-chemical parameters measured at the 4 streams on 10 occasions. *, ** indicate $p < 0.05$, 0.01, respectively.

| Parameter | $X^2$ values for Stream and Time Effects | | df |
|---|---|---|---|
| Discharge | 14.5** | 21.3** | 3,6 |
| % wet streambed | 24.5** | 19.7* | 3,9 |
| pH | 27.1** | 21.1* | 3,9 |
| Conductivity | 22.3** | 18.7* | 3,9 |
| Alkalinity | 28.6** | 18.7** | 3,9 |
| DOC | 16.9** | 21.8** | 3,9 |
| POC | 15.3** | 12.6 | 3,8 |

**Table 4.4.** Based on results of Friedman's two-way non-parametric ANOVA, order of streams from highest to lowest with respect to mean monthly values of selected physico-chemical parameters.

| Parameters | Order of streams |
|---|---|
| Discharge | Mapourika, Steep = Noone, Jetty. |
| % wet streambed | Noone, Mapourika = Steep, Jetty. |
| pH | Mapourika, Noone, Steep = Jetty. |
| Conductivity | Mapourika, Noone, Steep = Jetty. |
| Alkalinity | Mapourika, Noone, Steep = Jetty. |
| DOC | Noone = Steep, Jetty, Mapourika. |
| POC | Noone, Mapourika, Steep = Jetty. |

The proportion of the stream channel under water was also significantly different among streams, however, it was not related to the size of the catchment. Instead this measure of flow variability reflected differences in the physical slope, shape and structure of the stream channel. Thus Noone Creek had the lowest gradient and least variability in wetted channel whereas Jetty Creek was the steepest stream and exhibited greatest channel variability.

Temperature ranges in all streams showed a clear seasonal pattern. Summer maxima were greater in Mapourika and Jetty Creeks than in Noone and Steep Creeks, however, winter minima were similar in all streams. Summer maxima reflected differences in aspect of the streams and their exposure to the sun.

Significant differences in pH, conductivity, alkalinity, DOC and POC were found among the 4 streams. Streamwater pH was always highest in Mapourika Creek ($x = 6.1$). Jetty and Steep Creeks had more acidic waters ($x = 4.7$ and 4.6, respectively) whereas the pH at Noone Creek was intermediate ($x = 5.7$). Low coefficients of variation (4, 8, 3 & 7%, $n = 14$ for Noone, Mapourika and Jetty Creeks, and $n = 11$ for Steep Creek, respectively) indicate that pH of streamwater did not fluctuate markedly during the study.

Alkalinity also differed significantly among the streams, although temporal variation was high (CVs= 35, 58, 24, 43%, $n = 14$ for Noone, Mapourika, Jetty, Steep ($n = 11$) Creeks, respectively). Conductivity was also highest in Mapourika Creek, where pH and alkalinity were highest, and lowest in Jetty Creek. Because waters with low conductivity can dissolve more organic carbon than those with higher conductivities (Thurman 1985), low DOC concentrations in Mapourika Creek may reflect that stream's higher ionic conductance.

Furthermore, minor differences in catchment topography and geology, especially in soil profiles, may also be responsible for differences in water chemistry. The amount of organic material accumulated in riparian catchments has been shown to influence streamwater pH, conductivity and nutrient levels (Keithan & Lowe 1985).

B. Effect of flow on water chemistry parameters

Chemical responses to changes in stream discharge were investigated during the long term sampling program and by sampling flood events intensively in November-December 1984, April 1985, September 1985 and March 1986. During the regular sampling program, monitoring was generally undertaken for 3 to 5 days at a time and both rising and falling flows were sampled; most of the sampling trips occurred during falling flows.

(i) Long term sampling program

At Noone Creek (Table 4.5a) and Mapourika Creek (Table 4.5b), DOC and POC concentrations generally increased as discharge increased (ie. positive association with streamflows), but pH, conductivity and alkalinity all declined as discharges became higher. These responses were consistent during both rising and falling discharges, although increases in DOC concentration were often slightly delayed on the rising flows. Similar responses were shown by Jetty (Table 4.5c) and Steep Creeks (Table 4.5d), although at these sites discharge related changes in pH and conductivity were slighter.

Table 4.5. Changes in water chemistry recorded over 3-5 day periods (26 days - November 1984) in 14 months at a) Noone, b) Mapourika, c) Jetty and d) Steep Creeks. Changes are shown as '-' indicating negative association with increasing flow, '+' positive association, '0' no change or '?' data unavailable. Discharges either rose (R), fell (F) or both (B).

| | Nov 84 | Jan 85 | Mar | Apr | May | Jul | Aug | Sep | Oct | Nov | Jan 86 | Mar | May | Jul |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **a) Noone Ck.** | | | | | | | | | | | | | | |
| Discharge | B | B | F | B | R | F | F | F | B | F | F | B | F | F |
| pH | - | - | + | - | - | 0 | - | - | ? | + | - | - | - | - |
| Cond. | - | 0 | - | 0 | - | + | - | - | - | 0 | - | 0 | + | - |
| Alk. | - | - | 0 | - | - | + | - | 0 | ? | 0 | - | - | - | 0 |
| DOC | + | + | + | + | + | + | + | - | - | + | + | + | 0 | - |
| POC | ? | ? | ? | + | 0 | ? | 0 | + | + | + | 0 | 0 | 0 | - |
| **b) Mapourika Ck.** | | | | | | | | | | | | | | |
| Discharge | B | B | F | B | R | F | F | F | B | F | F | B | F | F |
| pH | - | - | + | - | - | + | - | + | ? | + | - | - | - | - |
| Cond. | - | - | + | - | - | + | - | - | - | - | - | - | - | - |
| Alk. | - | - | + | - | - | + | - | 0 | - | - | - | - | - | - |
| DOC | + | + | + | + | + | - | + | - | + | + | + | + | 0 | + |
| POC | ? | ? | ? | + | 0 | ? | + | + | + | + | + | + | 0 | + |
| **c) Jetty Ck.** | | | | | | | | | | | | | | |
| Discharge | B | B | F | B | R | F | F | F | B | F | F | B | F | F |
| pH | - | - | + | 0 | 0 | 0 | + | - | ? | 0 | - | - | - | - |
| Cond. | - | 0 | + | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | - | 0 |
| Alk. | - | - | - | - | 0 | + | - | - | - | - | 0 | - | - | 0 |
| DOC | + | + | + | + | + | + | + | - | + | + | + | + | 0 | + |
| POC | ? | ? | ? | + | + | ? | 0 | 0 | + | + | + | - | 0 | + |
| **d) Steep Ck.** | | | | | | | | | | | | | | |
| Discharge | ? | ? | ? | ? | R | F | F | F | B | F | F | B | F | F |
| pH | ? | ? | ? | ? | - | 0 | 0 | - | ? | - | - | - | - | - |
| Cond. | ? | ? | ? | ? | 0 | + | - | 0 | + | 0 | - | 0 | + | - |
| Alk. | ? | ? | ? | ? | - | - | - | 0 | + | - | - | - | - | - |
| DOC | ? | ? | ? | ? | + | 0 | + | - | + | + | 0 | + | - | + |
| POC | ? | ? | ? | ? | + | ? | - | + | + | 0 | + | 0 | - | + |

At each of the 4 streams, the frequency of positive associations between DOC and discharge, and POC and discharge and the negative associations between discharge and each of pH, alkalinity and conductivity, were significantly greater than expected by chance alone (Table 4.6, for Chi-square results).

Table 4.6. Results of Chi-square tests on the frequencies of associations between changes in water chemistry with increasing discharge. For all combinations, **= p< 0.01, *= p< 0.05; df= 3.

| Parameter | Noone | Mapourika | Jetty | Steep | Association |
|---|---|---|---|---|---|
| pH | 14.79** | 14.0** | 6.0ns | 11.6** | Negative |
| Alkalinity | 9.43* | 22.0** | 17.43** | 18.0** | Negative |
| Conductivity | 10.57** | 28.29** | 17.43** | 3.6ns | Negative |
| DOC | 17.43** | 22.0** | 27.7** | 7.6* | Positive |
| POC | 5.2ns | 15.6** | 6.8ns | 3.6ns | Positive |

(ii) Intensive sampling of flood events

A number of storm events occurred during sampling periods and changes in water chemistry were monitored intensively on five occasions. The storms were in November-December 1984 (two storm events, Noone, Mapourika and Jetty Creeks monitored), April 1985 (Noone, Mapourika and Jetty Creeks sampled), September 1985 (only Steep Creek monitored), and March 1986 (only Noone and Mapourika Creeks monitored). Water samples were collected up to 24 hours prior to the storm and at irregular intervals during the storm (except in November-December 1984). Frequency of sample collection, which was only carried out during daylight hours, depended upon the intensity of rainfall and apparent changes in streamflow.

a) November-December 1984

During the November-December 1984 sampling period, storm events occurred on 30 November and 4-5 December. Fifty, 101 and 64 mm of rain were recorded at Noone, Mapourika and Jetty Creeks, respectively during the first storm event (24 hours duration) and 177, 253 and 202 mm of rain were collected at these sites during the second storm event (also 24 hours duration). The different amounts of rainfall recorded at the three

conductivity, alkalinity and DOC) during the two storm events are shown in Table 4.7. At Noone Creek, decreases in all water chemistry parameters were observed during the first storm, whereas in Jetty Creek, pH and conductivity fell, alkalinity rose and DOC showed little change with increasing discharge. In Mapourika Creek, pH and alkalinity declined, but DOC increased with increasing flow and conductivity showed little change.

**Table 4.7.** Changes in water chemistry recorded during two storm events (30 November and 4-5 December 1984) at a) Noone, b) Mapourika and c) Jetty Creeks. ? = data unavailable.

| Site | Date | Time h | Rain. mm | Disch. l/s | pH | Cond. uS/cm | Alk. mg $CaCO_3$/l | DOC mg/l |
|---|---|---|---|---|---|---|---|---|
| a) | 30 Nov 84 | 1000 | 25 | 8.2 | 5.8 | 24.5 | 6.9 | 5.5 |
| | | 1400 | 25 | 82 | 4.6 | 20.5 | 2.1 | 3.4 |
| | 4 Dec 84 | 1000 | 0 | 0.8 | 5.7 | 18.3 | 4.2 | 5.5 |
| | | 1400 | 76 | 120 | 5.3 | 15.0 | 4.7 | 7.5 |
| | 5 Dec 84 | 1000 | 101 | 85 | 4.8 | 14.8 | 2.2 | 6.5 |
| b) | 30 Nov 84 | 1000 | 38 | 27 | 6.3 | 31.0 | 15.4 | 1.8 |
| | | 1400 | 63 | 130 | 6.0 | 29.5 | 5.1 | 6.7 |
| | 4 Dec 84 | 1000 | 0 | 7.5 | 6.4 | 31.0 | 15.3 | 1.6 |
| | | 1400 | 126 | 900 | 5.0 | 22.3 | 2.8 | 5.2 |
| | 5 Dec 84 | 1000 | 126 | 720 | 4.9 | 21.8 | 1.9 | ? |
| c) | 30 Nov 84 | 1000 | 32 | 1.3 | 4.3 | 20.0 | 1.0 | 5.8 |
| | | 1400 | 32 | 660 | 4.1 | 13.0 | 1.7 | 5.6 |
| | 4 Dec 84 | 1000 | 0 | 1.9 | 4.9 | 14.5 | 2.2 | 5.5 |
| | | 1400 | 76 | 660 | 4.6 | 13.8 | 1.6 | 6.7 |
| | 5 Dec 84 | 1000 | 126 | 175 | 4.8 | 13.8 | 1.4 | 6.5 |

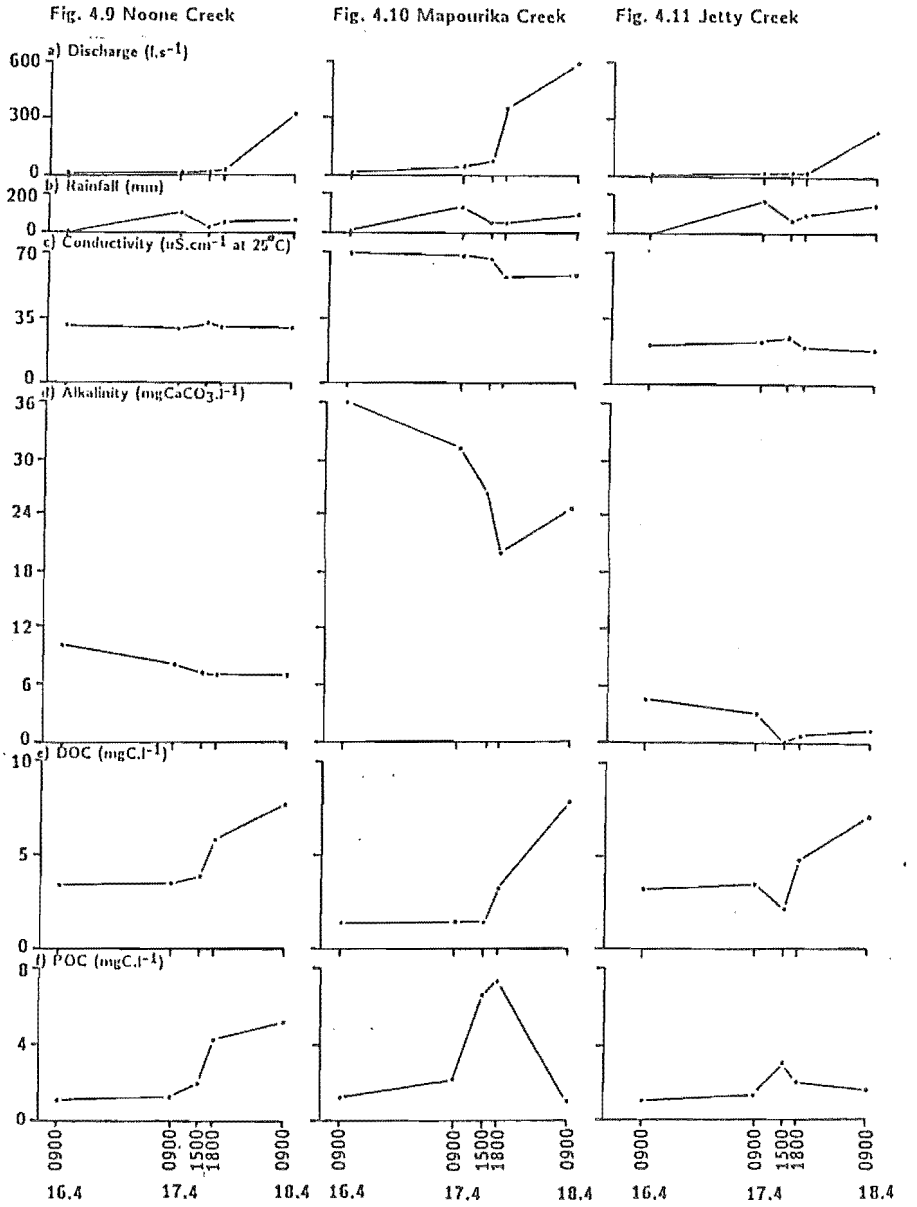
During the second storm event, DOC concentrations increased in all streams (up to 3.5 times), whereas pH, conductivity and alkalinity declined as flow increased.

b) April 1985

On 16-18 April about 274 mm of rain fell in the Lake Mapourika-Okarito River catchment and I was able to monitor changes in water chemistry as discharge increased at Noone, Mapourika and Jetty Creeks. However, some pH readings could not be made, because of a faulty meter.

Changes in water chemistry parameters as streamflow increased are shown in Figures 4.9-4.11. All three streams began to rise on 17 April and 40-200 times increases in discharge were recorded at the three streams during the storm event. Most changes in water chemistry parameters occurred early in the storm event as water was rising (between 0900 and 1800 h on 17 April). In all streams, concentrations of DOC increased with rising flows, whereas alkalinity decreased and conductivity showed little change except at Mapourika Creek, where there was a marked decrease. POC concentration at Noone Creek increased gradually with discharge, however, at Mapourika and Jetty Creeks, POC concentrations peaked 24 and 21 hours, respectively, from the start of the storm, despite continued increases in discharge. This may have been because less suspendable organic material was present on the beds of Mapourika and Jetty Creeks, where catchments are steep and particulate material is likely to be more rapidly flushed through the system. Overall, the magnitude of changes were such that DOC and POC in the water column doubled in the first 24 hours of the storm event in all streams.

Correlation coefficients between water chemistry parameters and discharge and rainfall are shown in Table 4.8. Although few correlations were significant, discharge was always positively associated with rainfall and DOC concentration in all streams, whereas alkalinity was negatively associated with discharge.




Figures 4.9-4.11. Changes in physico-chemical parameters measured during a storm event in April 1985 at Noone (Fig. 4.9), Mapourika (Fig. 4.10) and Jetty Creeks (Fig. 4.11). Parameters measured were a) discharge, b) rainfall, c) conductivity, d) alkalinity, e) DOC and f) POC. Labelling for all X-axes indicated on f).

Table 4.8. Spearman rank correlation coefficients between selected physico-chemical parameters recorded during a flood event in April 1985 at a) Noone, b) Mapourika and c) Jetty Creeks. For all correlations, n= 5; *= p< 0.05.

| | Disch. | Rain. | Cond. | Alk. | DOC | POC |
|---|---|---|---|---|---|---|
| a) Noone Ck. | | | | | | |
| Discharge | 1.000 | | | | | |
| Rainfall | 0.786 | 1.000 | | | | |
| Conductivity | -0.175 | -0.875 | 1.000 | | | |
| Alkalinity | -0.925* | -0.400 | 0.735 | 1.000 | | |
| DOC | 0.675 | 0.200 | -0.525 | -0.600 | 1.000 | |
| POC | 0.975* | 0.400 | -0.325 | -1.000* | 0.600 | 1.000 |
| b) Mapourika Ck. | | | | | | |
| Discharge | 1.000 | | | | | |
| Rainfall | 0.735 | 1.00 | | | | |
| Conductivity | -0.900* | -0.325 | 1.000 | | | |
| Alkalinity | -0.900* | -0.325 | 1.000* | 1.000 | | |
| DOC | 0.975* | 0.200 | -0.825 | -0.825 | 1.000 | |
| POC | 0.000 | 0.125 | -0.400 | -0.400 | 0.025 | 1.000 |
| c) Jetty Ck. | | | | | | |
| Discharge | 1.000 | | | | | |
| Rainfall | 0.400 | 1.00 | | | | |
| Conductivity | -0.700 | -0.200 | 1.000 | | | |
| Alkalinity | -0.100 | -0.000 | -0.200 | 1.000 | | |
| DOC | 0.900* | 0.600 | -0.900* | -0.100 | 1.000 | |
| POC | 0.300 | 0.000 | 0.200 | -1.000* | -0.100 | 1.000 |

c) September 1985

From 2 to 8 September, 230 mm of rain was recorded at Steep Creek. During this period, 9 streamwater samples were collected as discharge rose from 9 l/s to a peak of 886 l/s and then fell to 30 l/s. Results of physico-chemical analyses are shown in Figure 4.12. No conductivity readings were taken as the meter was not functioning at the time.

Flow responded rapidly to rainfall and both peaked at 0930 h on 4 September. Streamwater pH fell from 4.6 to 4.2 in the first 7 hours, and 17 hours later began to increase as discharge began to fall. Alkalinity initially fell in parallel with pH but regained its initial concentration after 34 hours when discharge had fallen to pre-storm levels. Both DOC and POC concentrations continued to increase gradually during the storm event even after the floodwaters began to recede. This suggests that rain may have facilitated the flushing or removal of organic material stored within the catchment. Significant positive correlations were found between rainfall and discharge and significant negative correlations were found between discharge and pH and discharge and alkalinity during the September storm at Steep Creek (Table 4.9).

**Table 4.9.** Spearman rank correlation coefficients between water chemistry and physiographic parameters recorded during a flood event in September 1985 at Steep Creek. For all combinations, n= 9; *= $p<0.05$

| | Disch. | Rain | pH | Alk. | DOC | POC |
|---|---|---|---|---|---|---|
| Discharge | 1.000 | | | | | |
| Rainfall | 0.750* | 1.00 | | | | |
| pH | -0.696* | -0.263 | 1.000 | | | |
| Alkalinity | -0.696* | -0.554 | 0.483 | 1.000 | | |
| DOC | -0.250 | -0.400 | 0.229 | 0.290 | 1.000 | |
| POC | -0.433 | -0.200 | 0.596 | 0.279 | 0.700* | 1.000 |

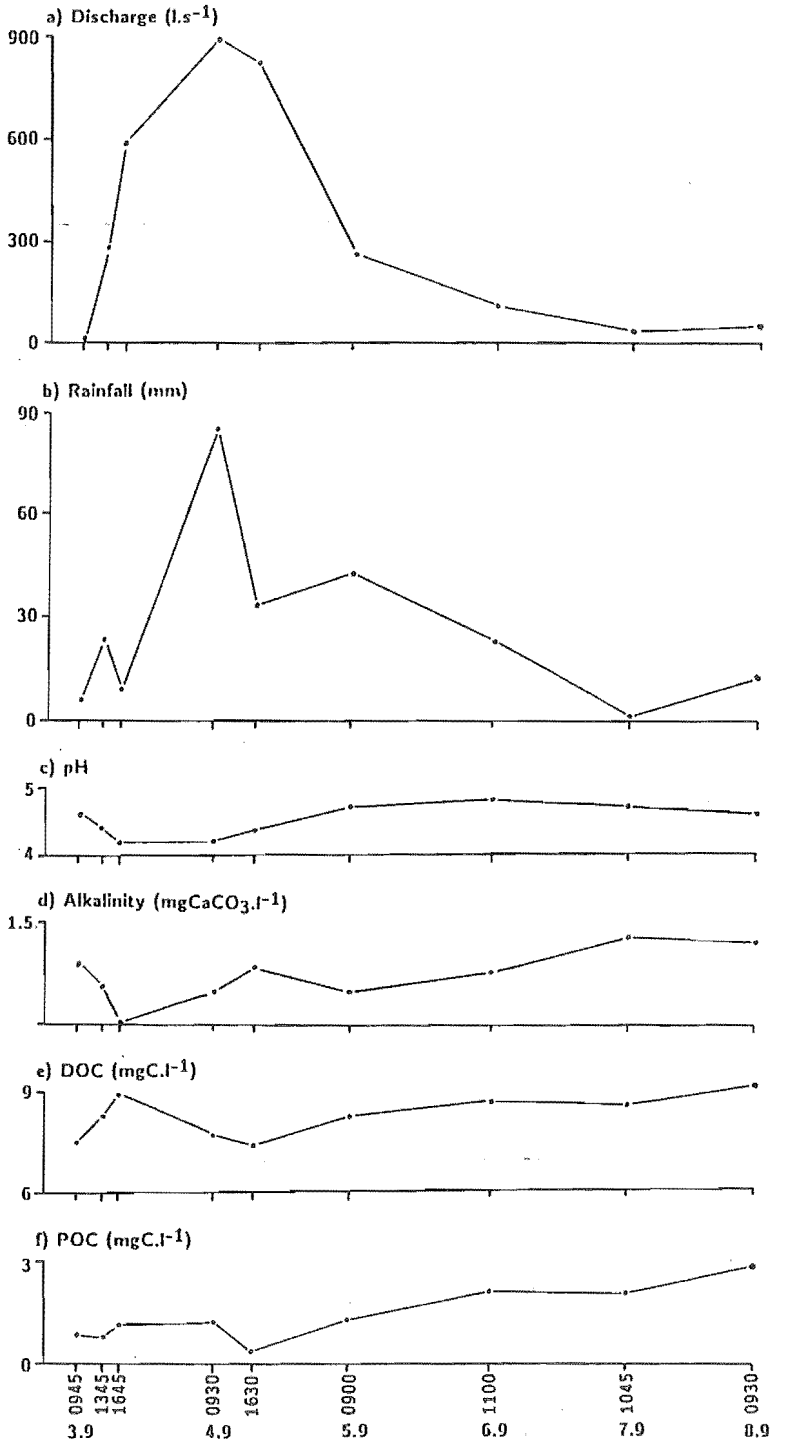
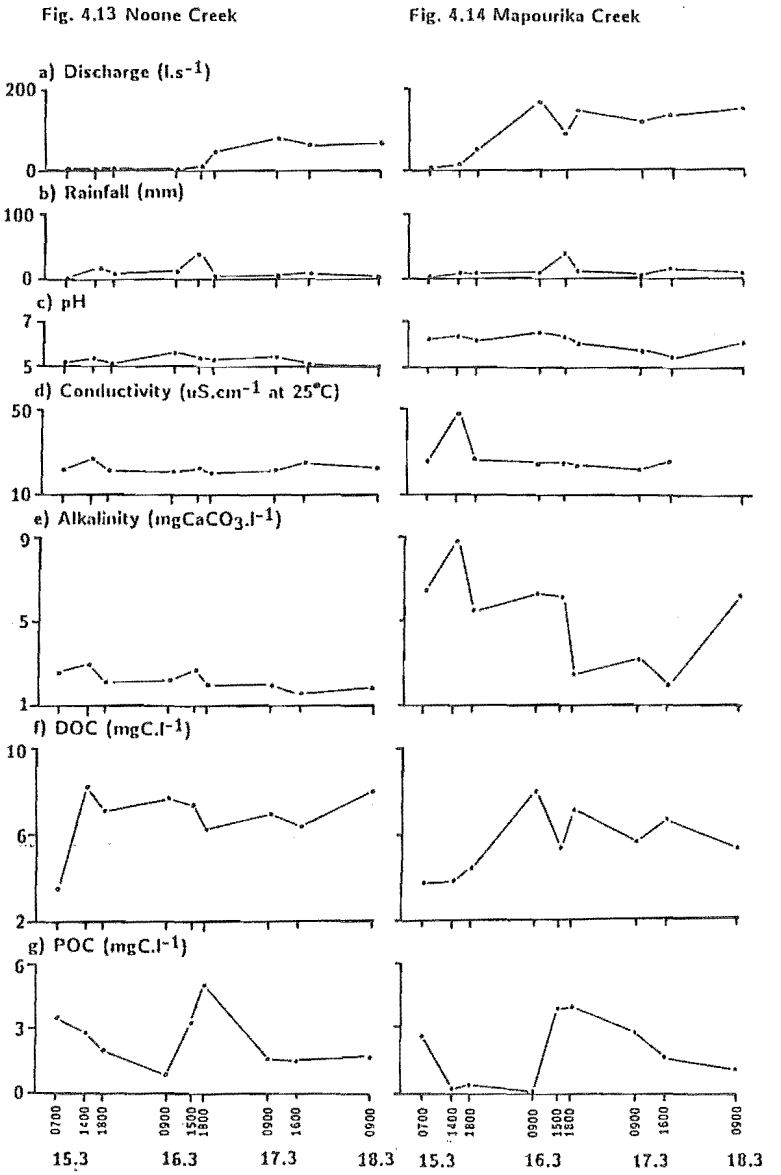



Figure 4.12. Changes in physico-chemical parameters measured during a storm event in September 1985 at Steep Creek. Parameters measured were a) discharge, b) rainfall, c) pH, d) alkalinity, e) DOC and f) POC. Labelling for all X-axes indicated on f).




Figures 4.13, 4.14. Changes in physico-chemical parameters measured during a storm event in March 1986 at Noone (Fig. 4.13) and Mapourika (Fig. 4.14) Creeks. Parameters measured were a) discharge, b) rainfall, c) pH, d) conductivity, e) alkalinity, f) DOC and g) POC. Labelling for all X-axes indicated on g).

d) March 1986

Between 15 and 18 March 1986, a 10-fold increase in discharge was recorded at Noone and Mapourika Creeks as 108 and 95 mm of rain fell at the two sites, respectively. However, the timing of rainfall and increases in discharge differed between the two streams. Noone Creek began to rise between 1500 and 1800 hours on 16 March after 53 mm of rain had been recorded, whereas Mapourika Creek rose sharply almost 24 hours prior to Noone Creek, when only 10 mm of rain had fallen at the sampling site. Discharge at Mapourika Creek dropped slightly between 0900 and 1800 h on 16 March, although 50 mm of rain was recorded during this period.

Therefore, discharge of both streams remained comparatively high, despite little rainfall being recorded at the sampling sites during this period. These results suggest that rainfall measured at the sampling site was not a good indicator of rainfall higher in the catchment.

Subsequent responses of the two streams differed considerably (Figs. 4.13 4.14). As discharge increased, pH fell slightly at Noone Creek, whereas at Mapourika Creek pH declined sharply and as a result a significant negative correlation was found between discharge and pH (Table 4.10).

Both conductivity and alkalinity at Noone Creek, and alkalinity at Mapourika Creek showed a positive association with rainfall since the previous readings were made, but a negative relationship with increasing discharge. After an initial peak in conductivity at Mapourika Creek, there was little change during the remainder of the storm event. DOC concentrations increased rapidly during the first 7 hours at Noone Creek and remained high thereafter. However, at Mapourika Creek the increase was more gradual and was related to discharge which was positively correlated with DOC concentration. At both streams, POC concentration

exhibited a similar pattern which involved an initial decrease, an increase to a peak following the period of maximum rainfall, and then a gradual decline.

**Table 4.10.** Spearman rank correlation coefficents between water chemistry and physiographic parameters measured at a) Noone and b) Mapourika Creeks during a flood event in March 1986. For all combinations, n= 9; *= p< 0.05.

| | Disch. | Rain | pH | Cond. | Alk. | DOC | POC |
|---|---|---|---|---|---|---|---|
| a) Noone Ck. | | | | | | | |
| Discharge | 1.000 | | | | | | |
| Rainfall | 0.304 | 1.00 | | | | | |
| pH | -0.433 | -0.570 | 1.000 | | | | |
| Conductivity | -0.488 | -0.420 | 0.529 | 1.000 | | | |
| Alkalinity | -0.746* | -0.588 | 0.550 | 0.113 | 1.000 | | |
| DOC | 0.520 | 0.488 | -0.250 | -0.379 | -0.283 | 1.000 | |
| POC | 0.267 | 0.054 | -0.283 | -0.063 | 0.000 | -0.667* | 1.000 |
| b) Mapourika Ck. | | | | | | | |
| Discharge | 1.000 | | | | | | |
| Rainfall | 0.823* | 1.00 | | | | | |
| pH | -0.318 | -0.845* | 1.000 | | | | |
| Conductivity | -0.400 | -0.271 | 0.520 | 1.000 | | | |
| Alkalinity | -0.379 | -0.500 | 0.737* | 0.571 | 1.000 | | |
| DOC | 0.871* | 0.000 | -0.146 | -0.696* | -0.567 | 1.000 | |
| POC | -0.038 | -0.233 | -0.438 | -0.604* | -0.533 | 0.133 | 1.000 |

e) Comparison among streams

The general effect of increased discharge on measured water chemistry parameters except POC was similar in all four streams (Table 4.6). Alkalinity, pH and conductivity were negatively associated with increasing discharge, whereas DOC and POC were positively correlated with discharge, although significantly so only at Mapourika Creek. However, despite these general similarities the streams differed in the magnitude of their responses to changes in discharge. At Mapourika Creek, pH and alkalinity always dropped markedly on rising flows, whereas Jetty and

Steep Creeks showed only a slight reduction and the response at Noone Creek was intermediate.

In low pH/high DOC stream systems such as Jetty and Steep Creeks, free $CO_2$ is the dominant form of inorganic carbon present and organic acids act as buffers rather than the $CO_2$-$HCO_3$-$CO_3$ system, which is the common buffering mechanism in freshwaters (Wetzel 1975). During periods of high rainfall, DOC is flushed into streams through the upper organic and organo-mineral soil horizons principally as organic acids which comprise up to 90% of the dissolved organic carbon in streamwater (Thurman 1985). Their effect on the already low pH and alkalinity levels is minimal, whereas in streams like Mapourika Creek, where pH and alkalinity levels are higher, these increases in organic acid concentrations result in much more marked reductions in pH and alkalinity of the stream water.

In contrast to DOC, no clear relationship between discharge and POC concentration was observed in any of the four study streams. A peak in POC concentration was observed during the April 1985 storm event at Mapourika Creek prior to maximum discharge, but this pattern was not observed during other storm events. Such a finding is not unexpected as storms occur frequently in this region of New Zealand and the amount of detritus stored within streambeds is characteristically low.

C. Summary of physico-chemical conditions

The four South Westland streams were flood-prone and experienced marked and rapid fluctuations in discharge in response to the high rainfall. No seasonality in flow patterns was observed. Discharge differences among the streams appeared to reflect their different slopes and catchment sizes.

Mapourika and Jetty Creeks had higher maximum water temperatures than Noone and Steep Creeks. Their catchments face Lake Mapourika and receive the uninterrupted afternoon sun, whereas Noone and Steep Creeks are shaded by the surrounding hills as they flow into Okarito River.

All four streams had brown, acidic waters (pH 4.5-6.5) with little bicarbonate buffering capacity and moderate to high concentrations of dissolved organic carbon (4-9 $mg.l^{-1}$). Streamwater pH, conductivity and alkalinity were highest in Mapourika Creek and lowest in Jetty and Steep Creeks. All three parameters decreased with increasing discharge as indicated by long-term and intensive sampling of storm events. DOC was greatest in Noone and Steep Creeks and lowest in Mapourika Creek and in contrast to pH, conductivity and alkalinity, DOC concentration was positively correlated with discharge. Quantitative differences among streams in the chemical factors measured must reflect differences in the topography, geology and soils of their upper catchments.

# Chapter Five

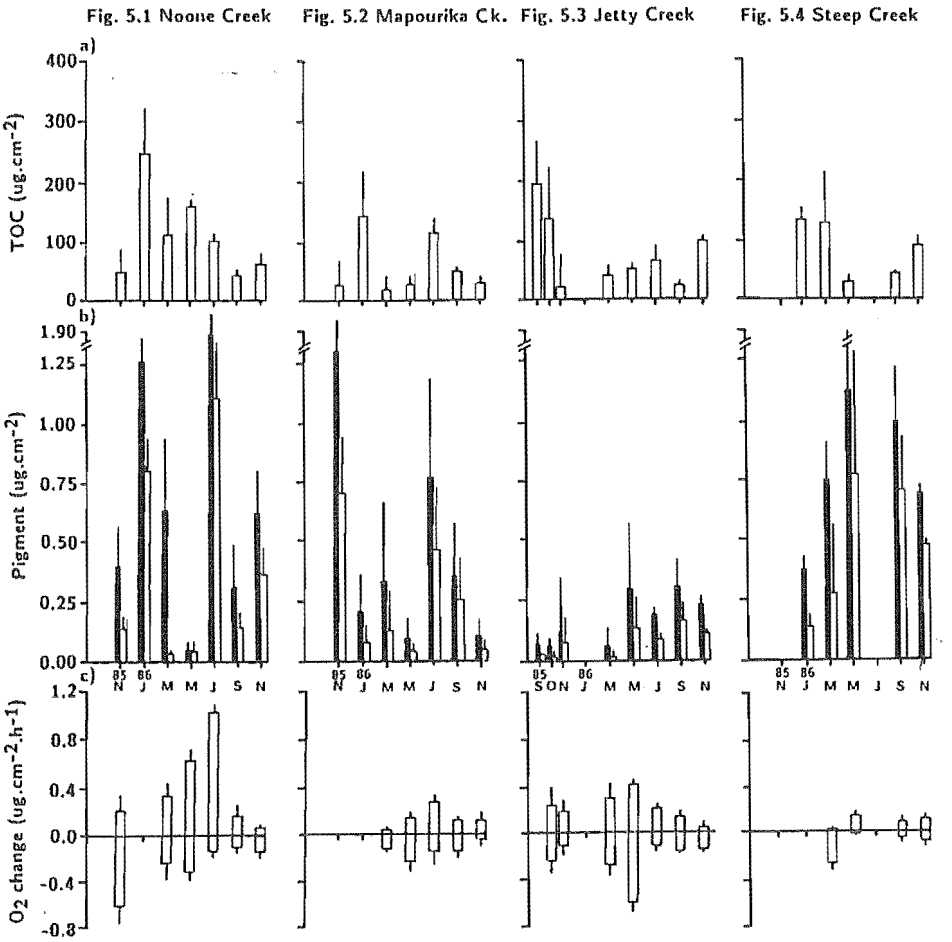
## INSTREAM PROCESSING AND RETENTION OF ORGANIC MATERIAL

### A. Structure, biomass and metabolic activity of epilithon

Stone surface organic layers were monitored regularly in the four streams (Noone, Mapourika, Jetty and Steep Creeks) from November 1985 to November 1986. Tiles were collected every two months, except in September and October 1985, when they were collected from Jetty Creek after only 30 days. No tiles were collected from Jetty Creek in January 1986 or Steep Creek in November 1985 and January 1986 because of heavy rainfall and subsequent high flows which washed the tiles away. Temporal changes in structure, biomass, primary production and respiration of epilithon in each stream are described below.

#### (i) Noone Creek

Temporal changes in epilithic standing crop, primary production rates and rates of community respiration are shown in Figure 5.1 a-c. Organic carbon content of epilithon ranged from 43 to 245 $ug.cm^{-2}$ and was greatest in January 1986. Chlorophyll *a* and total pigment (chlorophyll *a* plus phaeophytin) concentrations ranged from 0.04 to 1.41 and 0.05 to 1.88 $ug.cm^{-2}$, respectively. Chlorophyll *a* and total pigment exhibited similar temporal patterns and were highest in July 1986. Net community primary production (NCPP) was highest in July 1986, when pigment concentrations and by extrapolation algal biomass, were greatest. Community respiration rates (CR) were highest in November 1985 and ranged from 0.08 to 0.60 ug $O_2.cm^{-2}.h^{-1}$.




Figures 5.1-5.4. Values of epilithic parameters measured on tiles collected between September 1985 and November 1986 from Noone (Fig. 5.1), Mapourika (Fig. 5.2), Jetty (Fig. 5.3) and Steep Creeks (Fig. 5.4). Labelling for all X-axes indicated on b).

a) Mean TOC concentrations (±2SE) on 5 tiles.
b) Mean concentration (±2SE) of total photosynthetic pigments (shaded histograms) and chlorophyll *a* (open histograms) on 4 tiles.
c) Mean rates (±2SE) of net $O_2$ evolution and community respiration obtained from 5 tiles incubated under light and dark conditions.

Table 5.1. Spearman rank correlation coefficients between biological measures of the epilithic layers and physiographic parameters recorded at the four sites. For all combinations, * denotes $p < 0.05$.

| | TOC | Tot Pig | Chl a | CR | NCPP |
|---|---|---|---|---|---|
| a) **Noone Creek** | n=7 | n=7 | n=7 | n=6 | n=6 |
| Incubation period | 0.277 | 0.080 | -0.188 | -0.043 | -0.100 |
| Rainfall during prev. week | -0.750* | 0.250 | -0.429 | 0.714 | 0.543 |
| Total rainfall | 0.000 | 0.893* | 0.643 | -0.080 | 0.257 |
| Rain days during prev. week | -0.607 | 0.500 | -0.071 | 0.714 | 0.257 |
| Total rain days | 0.348 | 0.169 | 0.330 | -0.143 | 0.029 |
| Storms during prev. week | -0.277 | 0.170 | 0.098 | 0.643 | -0.186 |
| Total storms | 0.179 | 0.125 | -0.143 | -0.100 | -0.243 |
| b) **Mapourika Creek** | n=7 | n=7 | n=7 | n=6 | n=6 |
| Incubation period | 0.134 | -0.723* | -0.652 | -0.425 | -0.425 |
| Rainfall during prev. week | -0.857* | -0.214 | -0.214 | 0.200 | -0.200 |
| Total rainfall | -0.179 | -0.036 | -0.036 | -0.200 | 0.200 |
| Rain days during prev. week | -0.786* | 0.036 | 0.036 | -0.100 | -0.300 |
| Total rain days | 0.169 | -0.813* | -0.813* | -0.100 | 0.100 |
| Storms during prev. week | -0.277 | 0.116 | 0.116 | -0.300 | 0.100 |
| Total storms | -0.161 | -0.750* | -0.750* | -0.625 | -0.675 |
| c) **Jetty Creek** | n=8 | n=8 | n=8 | n=7 | n=7 |
| Incubation period | 0.527 | 0.339 | 0.241 | 0.529 | 0.071 |
| Rainfall during prev. week | -0.679* | -0.452 | -0.607 | 0.371 | 0.829* |
| Total rainfall | 0.071 | 0.119 | -0.107 | -0.429 | -0.086 |
| Rain days during prev. week | -0.741* | -0.661* | -0.866* | -0.029 | 0.429 |
| Total rain days | 0.714* | 0.429 | 0.393 | 0.371 | 0.029 |
| Storms during prev. week | -0.080 | 0.000 | -0.170 | -0.414 | -0.186 |
| Total storms | 0.580 | 0.232 | 0.170 | -0.557 | -0.014 |
| d) **Steep Creek** | n=5 | n=5 | n=5 | n=4 | n=4 |
| Incubation period | 0.425 | -0.075 | 0.375 | 0.350 | 0.350 |
| Rainfall during prev. week | -0.900* | -0.300 | -0.600 | 0.400 | -0.200 |
| Total rainfall | -0.200 | -0.900* | -0.800 | 0.600 | 0.000 |
| Rain days during prev. week | -0.675 | -0.625 | -0.775 | 0.650 | -0.250 |
| Total rain days | 0.375 | -0.375 | -0.075 | 0.000 | 0.600 |
| Storms during prev. week | 0.300 | -0.300 | -0.100 | 0.350 | 0.350 |
| Total storms | 0.075 | -0.375 | -0.275 | 0.600 | 0.000 |

Correlation coefficients between biological and physico-chemical parameters measured at Noone Creek are shown in Table 5.1. Only two correlations were significant ($p<0.05$). First, TOC levels were correlated negatively with rainfall recorded within the week prior to

sampling, and second total pigment concentrations were correlated negatively with total rainfall recorded during the incubation period.

Scanning electron microscopy of epilithic layers showed that throughout the study period their structure remained similar, although high discharge lowered the apparent diversity and abundance of colonizing organisms (Plate 5.1). The amorphous organic slime matrix covering the surfaces of tiles was colonized by bacterial rods and cocci, diatoms, blue-green algae, aquatic Hyphomycetes and Actinomycetes and filamentous green algae (*Tribonema*, *Oedogonium* and *Coleochaete*). Flocculated organic particles and other debris accumulated in many hollows and crevices. Diatom genera that were commonly recorded, were *Cocconeis*, *Achnanthes*, *Cymbella*, *Eunotia*, *Frustulia*, *Fragilaria*, *Navicula* and *Surirella*.

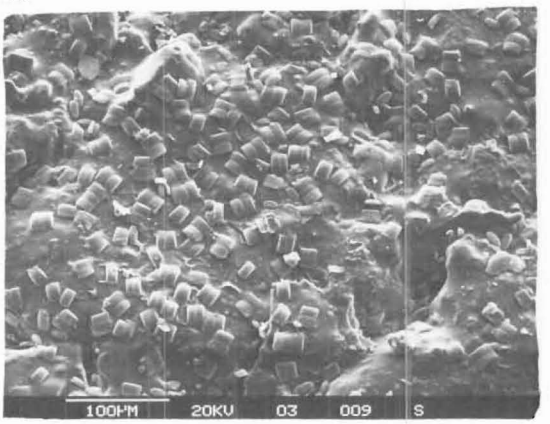
(ii) Mapourika Creek

Temporal changes in epilithic standing crop, production and respiration are shown in Figure 5.2 a-c. No seasonal patterns were apparent, and temporal variability was high. TOC concentrations ranged from 19 to 142 ug.cm$^{-2}$ and were highest in January 1986 as at Noone Creek. Chlorophyll *a* and total pigment concentrations ranged from 0.04 to 0.71, 0.10 to 1.31 ug.cm$^{-2}$, respectively and were greatest in November 1985. NCPP ranged from 0.04 to 0.28 ug $O_2$.cm$^{-2}$.h$^{-1}$ and peaked in July 1986. CR ranged from 0.05 to 0.23 ug $O_2$.cm$^{-2}$.h$^{-1}$ and was highest in May 1986.

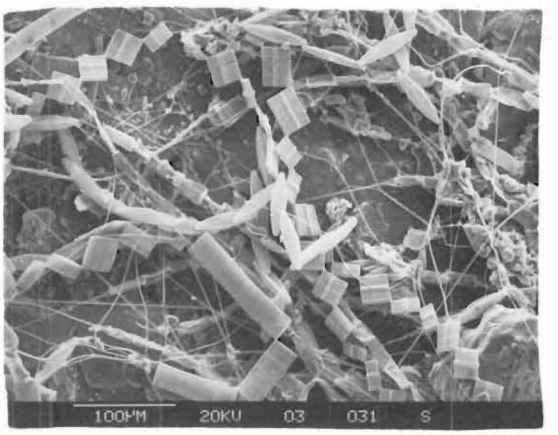
Seven statistically significant correlations ($p<0.05$) were found between measured biological and physico-chemical parameters (Table 5.1). The strongest was a negative correlation between TOC concentration and rainfall recorded within the week prior to sampling.

Plate 5.1. Scanning electron micrographs of epilithon colonizing the upper surfaces of tiles in Noone Creek. *Fragilaria ?vaucheriae* (A,D,E) was the most abundant diatom, although other diatoms were present: mostly *Taballaria* spp. (B), *Navicula* sp., *Cocconeis* spp. (F), *Surirella* (D), *Eunotia* spp. (D) and *Frustulia* sp. (C). Filamentous algae were commonly seen at this site, ie. *Coleochaete* (C), as were Actinomycetes (B) and bacterial rods and cocci (E,F).

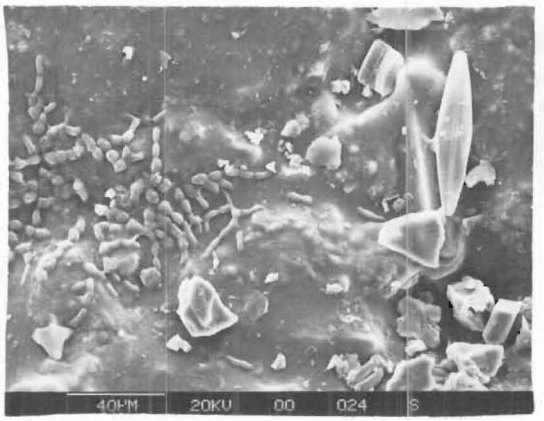
A


100PM 20KV 03 009 S

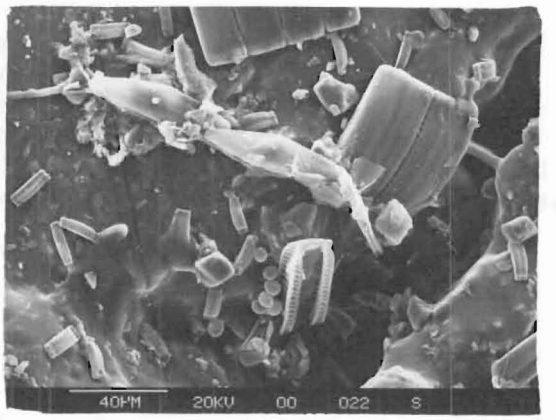
B


100PM 20KV 03 031 S

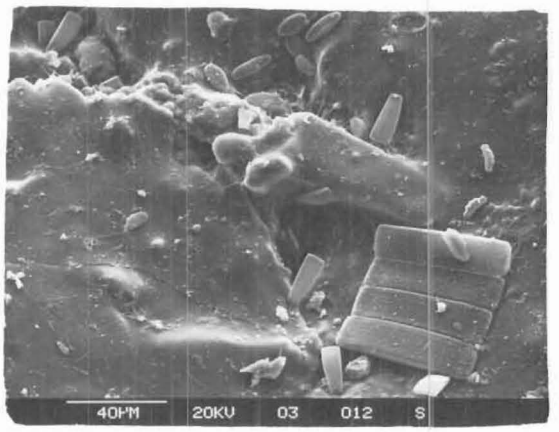
C


40PM 20KV 00 024 S

D


40PM 20KV 00 022 S

E


40PM 20KV 03 012 S

F

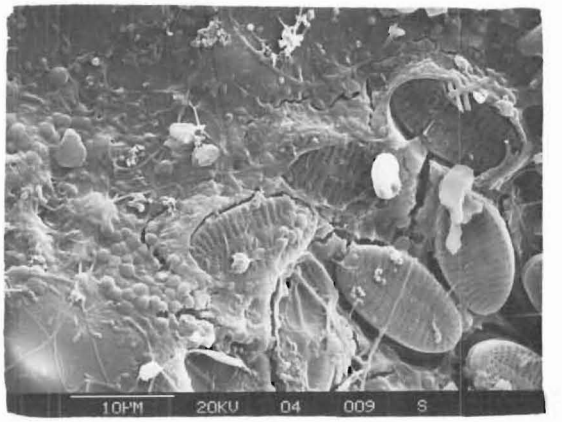
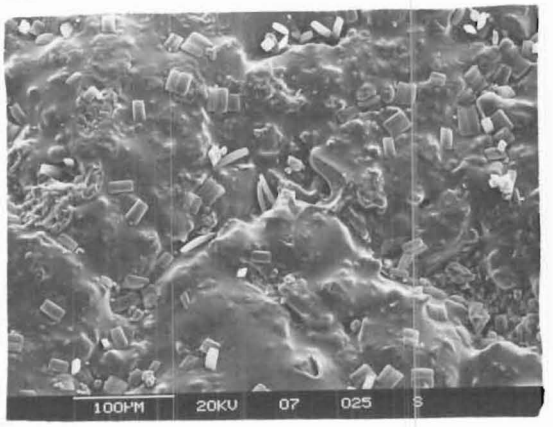
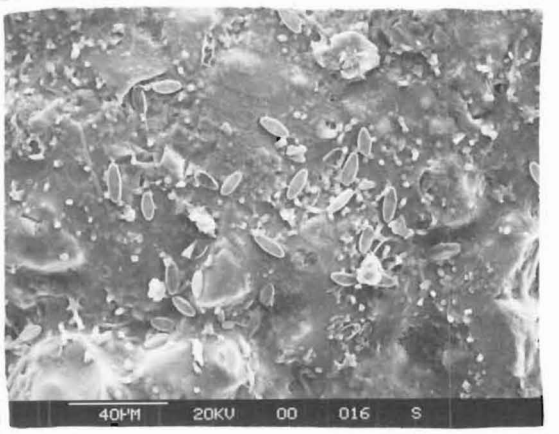

10PM 20KV 04 009 S

**Plate 5.2.** Scanning electron micrographs of epilithon colonizing the upper surfaces of tiles in Mapourika Creek. Amorphous material and blue green algae were often seen on the slime surfaces at this site (C,E,F). Although diatoms were less abundant at this site than Noone Creek, species of *Fragilaria* (A,B,C), *Cocconeis* (E,F) and *Navicula* (B,D) were commonly seen.

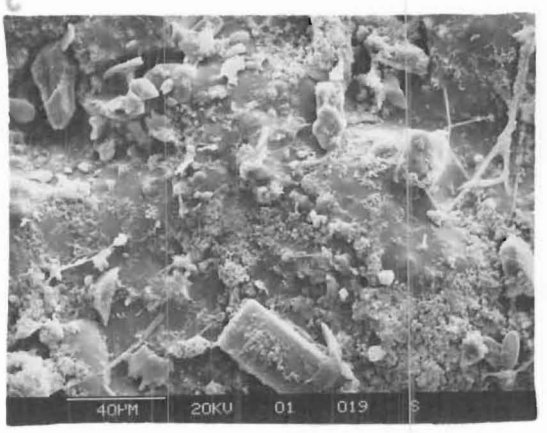
A


100µM 20KV 07 025 S

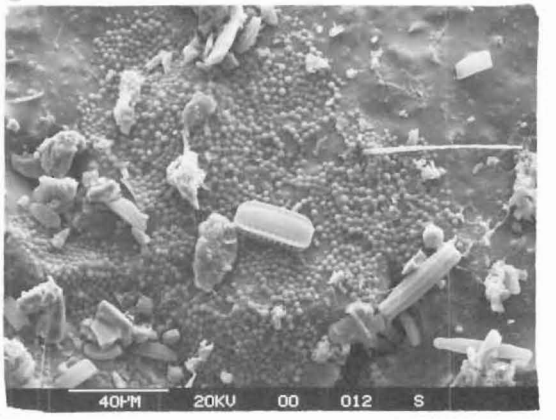
B


40µM 20KV 00 016 S

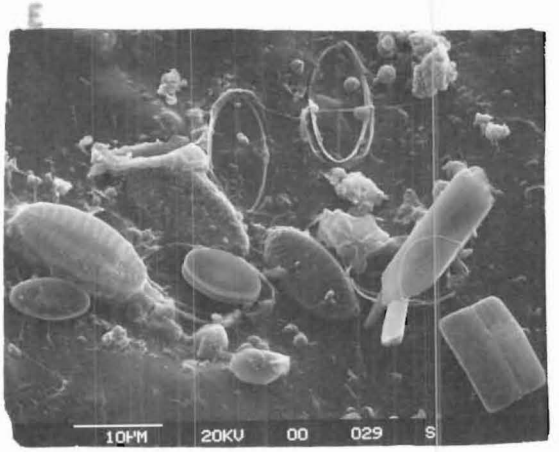
C


40µM 20KV 01 019 S

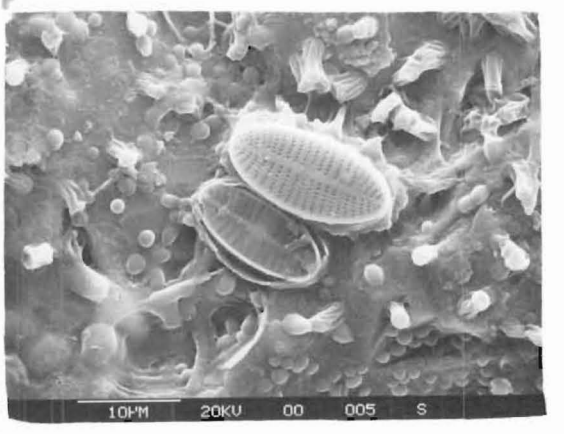
D


40µM 20KV 00 012 S

E


10µM 20KV 00 029 S

F


10µM 20KV 00 005 S

Scanning electron micrographs showed that the composition of the layers varied greatly over time (Plate 5.2). The amorphous organic slime matrix was generally well colonized by bacterial rods and cocci, however, only a few diatom genera (*Cocconeis*, *Eunotia* and *Fragilaria*), were commonly present. Colonization by diatoms was greatest in November 1985, March, May and November 1986, months characterized by low rainfall and low flow conditions.

(iii) Jetty Creek

Changes in epilithic standing crop, production and respiration measured during the year are shown in Figure 5.3 a-c. Temporal variability was high, but no seasonal patterns were apparent.

TOC concentrations ranged from 23 to 197 ug.cm$^{-2}$ and were highest in September 1985. Chlorophyll *a* and total pigment concentrations ranged from 0.02 to 0.17 and 0.07 to 0.31 ug.cm$^{-2}$ and maximum concentrations were found in September 1986. NCPP ranged from 0.04 to 0.41 ug $O_2$.cm$^{-2}$.h$^{-1}$ and was highest in May 1986 and lowest in November 1986. CR ranged from 0.12 to 0.61 ug $O_2$.cm$^{-2}$.h$^{-1}$ and also peaked in May 1986.

Six significant correlations were found between biological measures and physico-chemical parameters (Table 5.1). The strongest negative correlation was between chlorophyll *a* concentration and number of rain days recorded within the week prior to sampling. The strongest positive correlation was between oxygen production rate and the amount of rainfall recorded within the week prior to sampling.

Epilithic layers had a very simple structure throughout the study period (Plate 5.3). The amorphous organic slime matrix was covered with bacteria, flocculated organic particles and small numbers of *Eunotia*.

Other diatoms were rare except in September and November 1986 when *Fragilaria* and *Surirella*, were abundant.

(iv) Steep Creek

Temporal changes in epilithic standing crops, production and respiration measured on tiles are shown in Figure 5.4 a-c. Temporal variability of all biological parameters was high, and no seasonal trends were apparent.

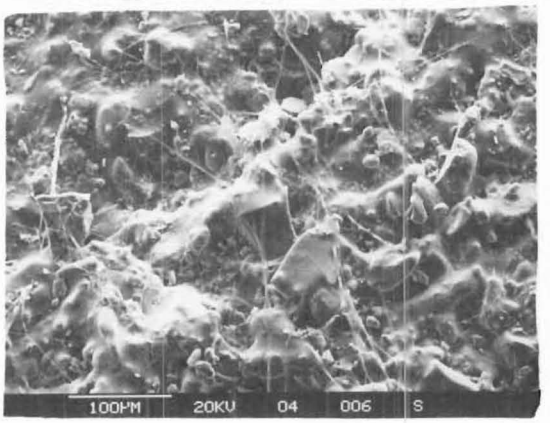
Organic carbon content on tiles ranged from 23 to 130 $ug.cm^{-2}$ and as at Noone and Mapourika Creeks was highest in January 1986. Chlorophyll *a* and total pigment concentrations ranged from 0.14 to 0.78, and 0.38 to 1.13 $ug.cm^{-2}$, respectively, and were greatest in May 1986. NCPP ranged from 0.02 to 0.13 ug $O_2.cm^{-2}.h^{-1}$ and was also highest in May 1986 when maximum pigment concentrations were recorded. CR rates ranging from 0.02 to 0.28 ug $O_2.cm^{-2}.h^{-1}$, were lowest in May 1986 and highest in March 1986.

Two significant correlations were found between biological and physico-chemical parameters (Table 5.1). The two negative correlations were between TOC concentration and rainfall recorded within the week prior to sampling and between total pigment concentration and total rainfall recorded during the tile incubation period.

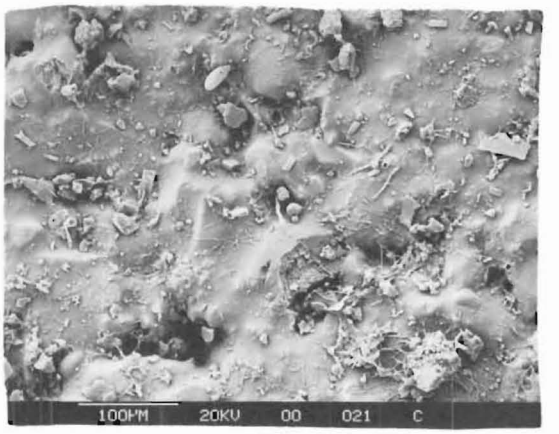
Composition of epilithic layers was similar to that observed in Mapourika Creek, although diatoms were more abundant (Plate 5.4). On most tiles, an amorphous organic slime layer was colonized by bacterial rods and cocci, filamentous blue-green algae and diatoms. Commonly recorded diatom genera were *Cocconeis*, *Eunotia*, *Navicula* and *Surirella*.

**Plate 5.3.** Scanning electron micrographs of epilithon colonizing the upper surfaces of tiles in Jetty Creek. Tile surface was colonized predominantly by bacteria and threads (fungi and Actinomycetes - A,F), although diatoms (mainly *Fragilaria ?vaucheriae* - B) and filamentous algae (*Coleochaete* - B,E,F) were abundant in September and November 1986 (D). Diatoms were often seen in the hollows and crevices of the slime layer (C).

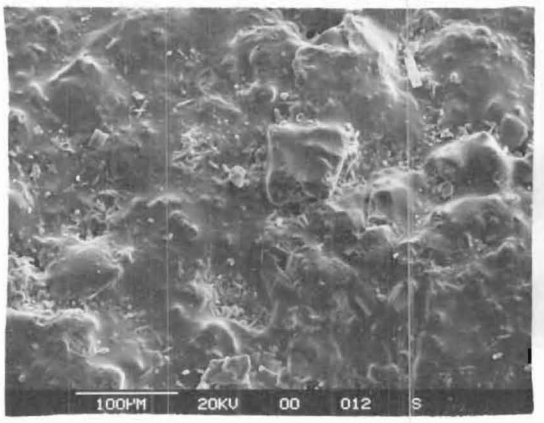
A


100µM 20KV 04 006 S

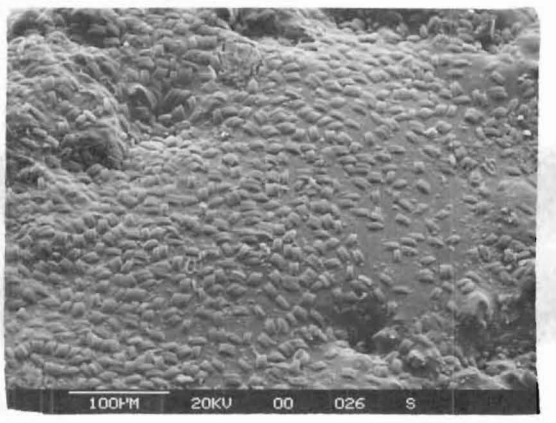
B


100µM 20KV 00 021 C

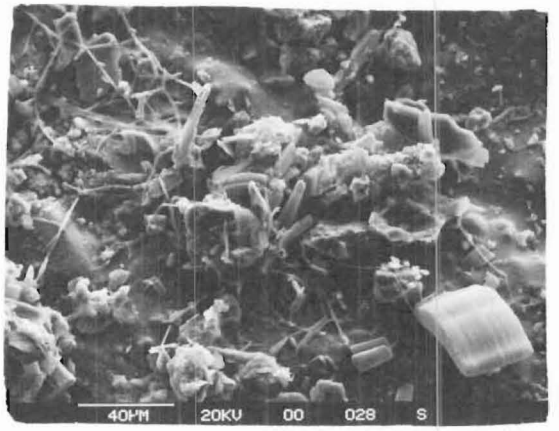
C


100µM 20KV 00 012 S

D


100µM 20KV 00 026 S

E


40µM 20KV 00 028 S

F

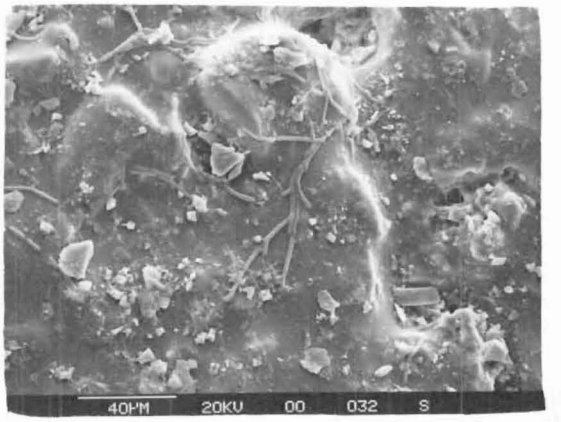
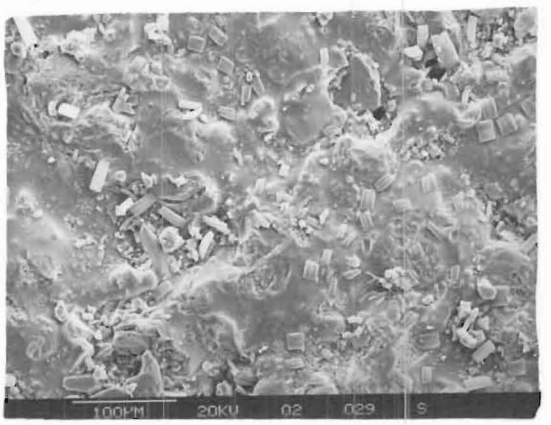
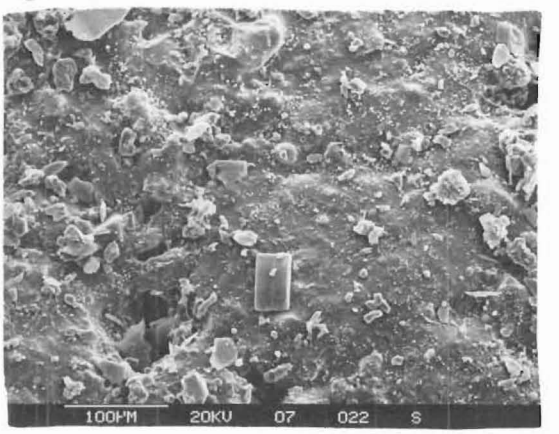

40µM 20KV 00 032 S

**Plate 5.4.** Scanning electron micrographs of epilithon colonizing the upper surfaces of tiles in Steep Creek. *Fragilaria ?vaucheriae* (A,C,D), *Eunotia* spp. (A,D) and *Surirella* (E) were the most common diatoms at this site. Filamentous algae (*Coleochaete, ?Lyngbya*) were rarely abundant (D,E), but blue green algae (B) and bacteria (B,F) were commonly seen on the tiles.

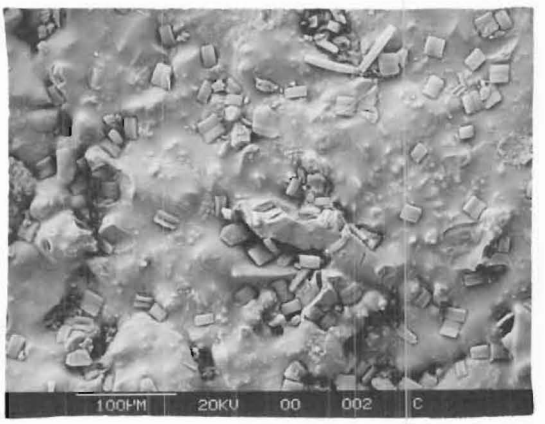
A


100µM 20KV 02 029 S

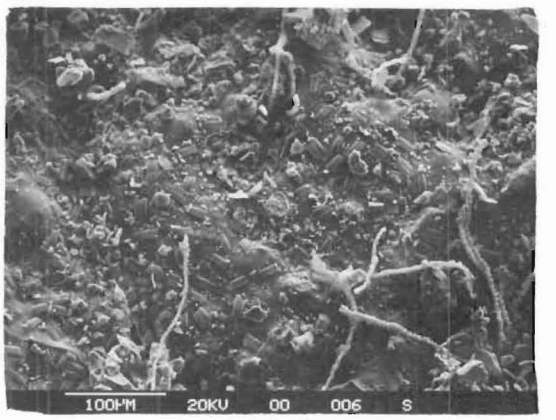
B


100µM 20KV 07 022 S

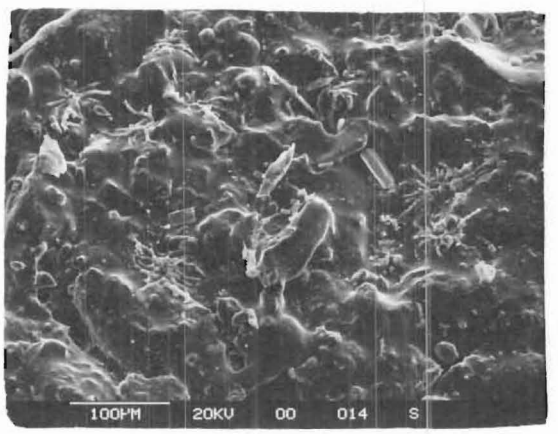
C


100µM 20KV 00 002 C

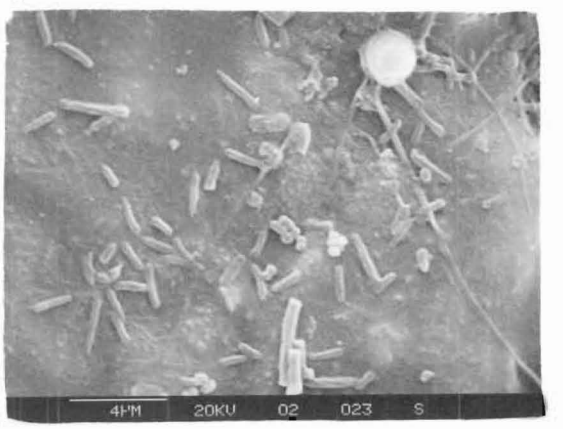
D


100µM 20KV 00 006 S

E


100µM 20KV 00 014 S

F


4µM 20KV 02 023 S

(v) Comparisons among streams

Organic carbon content of stone surface layers on tiles was similar in all four streams; mean TOC levels were between 64 and 111 ug.cm$^{-2}$. Epilithic standing crops measured in these four brownwater streams, were therefore within the range reported from other streams in the South Island of New Zealand (Cowie 1980, Rounick & Winterbourn 1983a, Collier 1988a,b). However, considerable variation in epilithic biomass was observed over time and no seasonal patterns were apparent.

In all streams, the amount of TOC present on tiles was negatively correlated with rainfall recorded within the week prior to sampling and indicates that recent flow conditions have an important influence on epilithic biomass. The streams lie in a region of high and frequent rainfall (annual rainfall= 5236 mm;177 raindays per year) and experience widely fluctuating discharge regimes. The frequent occurrence of high flows appears to be largely responsible for maintaining low epilithic standing crops as was found by Scrimgeour & Winterbourn (in press) in the much larger Ashley River, on the eastern side of the South Island, New Zealand.

Concentrations of chlorophyll *a* on tiles followed a similar pattern to total pigment concentrations in all streams. On most occasions, pigment concentrations were highest in Noone and Steep Creeks and lowest in Jetty Creek, however, there were no similarities in temporal patterns among streams. In contrast with the findings of Collier (1988a,b) and Mulholland *et al.* (1986), no association was found between streamwater pH and the autotrophic component of the stone surface layers as measured by chlorophyll *a* concentration. However, chlorophyll *a* concentration was positively correlated with epilithic carbon concentration (Table 5.2)

suggesting that fluctuations in flow influenced algal abundances, even if only weakly.

Table 5.2. Spearman rank correlation coefficients between measured biological parameters combined from all streams. For all combinations, n= 27, except those involving community respiration (CR) and net community photosynthetic rates (NCPP) when n= 23. *, ** denote $p<0.05$ and $p< 0.01$, respectively.

| | TOC | Tot Pig | Chl a | CR | NCPP |
|---|---|---|---|---|---|
| TOC | 1.000 | | | | |
| Tot.Pig | 0.109 | 1.000 | | | |
| Chl.a | 0.352* | 0.893** | 1.000 | | |
| CR | -0.306 | -0.361* | -0.435* | 1.000 | |
| NCPP | -0.265 | -0.219 | -0.287 | 0.396* | 1.000 |

Table 5.3. Ratios of a) community respiration (CR) and b) gross primary production rate (GPP= CR+NCPP) to organic carbon (TOC) of epilithic layers for all sites and sampling dates.

| Sites: | Noone | Mapourika | Jetty | Steep |
|---|---|---|---|---|
| a) **CR:TOC** | | | | |
| 1985 October | - | - | 1:553 | - |
| November | 1:83 | - | 1:197 | - |
| 1986 March | 1:498 | 1:143 | 1:153 | 1:446 |
| May | 1:511 | 1:116 | 1:89 | 1:1000 |
| July | 1:811 | 1:752 | 1:558 | - |
| September | 1:506 | 1:336 | 1:155 | 1:578 |
| November | 1:481 | 1:638 | 1:656 | 1:956 |
| Overall mean: | 1:449 | 1:448 | 1:334 | 1:702 |
| b) **GPP:TOC** | | | | |
| 1985 October | - | - | 1:288 | - |
| November | 1:177 | - | 1:78 | - |
| 1986 March | 1:194 | 1:109 | 1:76 | 1:417 |
| May | 1:166 | 1:72 | 1:53 | 1:153 |
| July | 1:86 | 1:266 | 1:209 | - |
| September | 1:162 | 1:183 | 1:86 | 1:258 |
| November | 1:302 | 1:182 | 1:523 | 1:443 |
| Overall mean: | 1:165 | 1:226 | 1:178 | 1:406 |

Generally, net primary production rates were greater than respiration rates in all streams, although rates for both were low on a world-wide scale (Bott *et al.* 1985). Ratios of GPP:TOC and CR:TOC were also low by comparison with other stream studies (Bott *et al.* 1985) and indicate that the organic carbon content of the epilithic layers included a relatively large component with little biological activity (Table 5.3). Much of this latter carbon appears to be physically or abiotically adsorbed on to stone surfaces as indicated by Collier (1988).

B. Epilithic development - Series I & II

The structure of epilithon developing on tiles was investigated in Noone, Mapourika and Jetty Creeks on two occasions. Tiles were placed in the streams in November 1984 (Series I) and March 1985 (Series II) and removed after approximately 10, 20, 30 and, where possible, 60 days. No tiles could be collected from Noone and Jetty Creeks in January 1985 or Mapourika Creek in May 1985 because heavy flooding washed them away.

(i) Noone Creek

a) Series I

Development of epilithic biomass on tiles from series I is shown in Figure 5.5a. Organic carbon content built up rapidly in the first 16 days and remained relatively constant thereafter. Scanning electron micrographs showed a complementary pattern of organic layer development, with tile surfaces being covered by an amorphous, organic matrix or "slime" layer within 9 days when flocculated organic particles were also present (Plate 5.5). By day 16, the layer also incorporated bacterial rods and cocci, hyphae of aquatic fungi and a blue-green alga *Lyngbya*. Low densities of *Surirella* and *Cocconeis* were also apparent. Diatom

colonization was greater by day 28 when species of *Eunotia*, *Surirella* and *Cocconeis* were abundant.

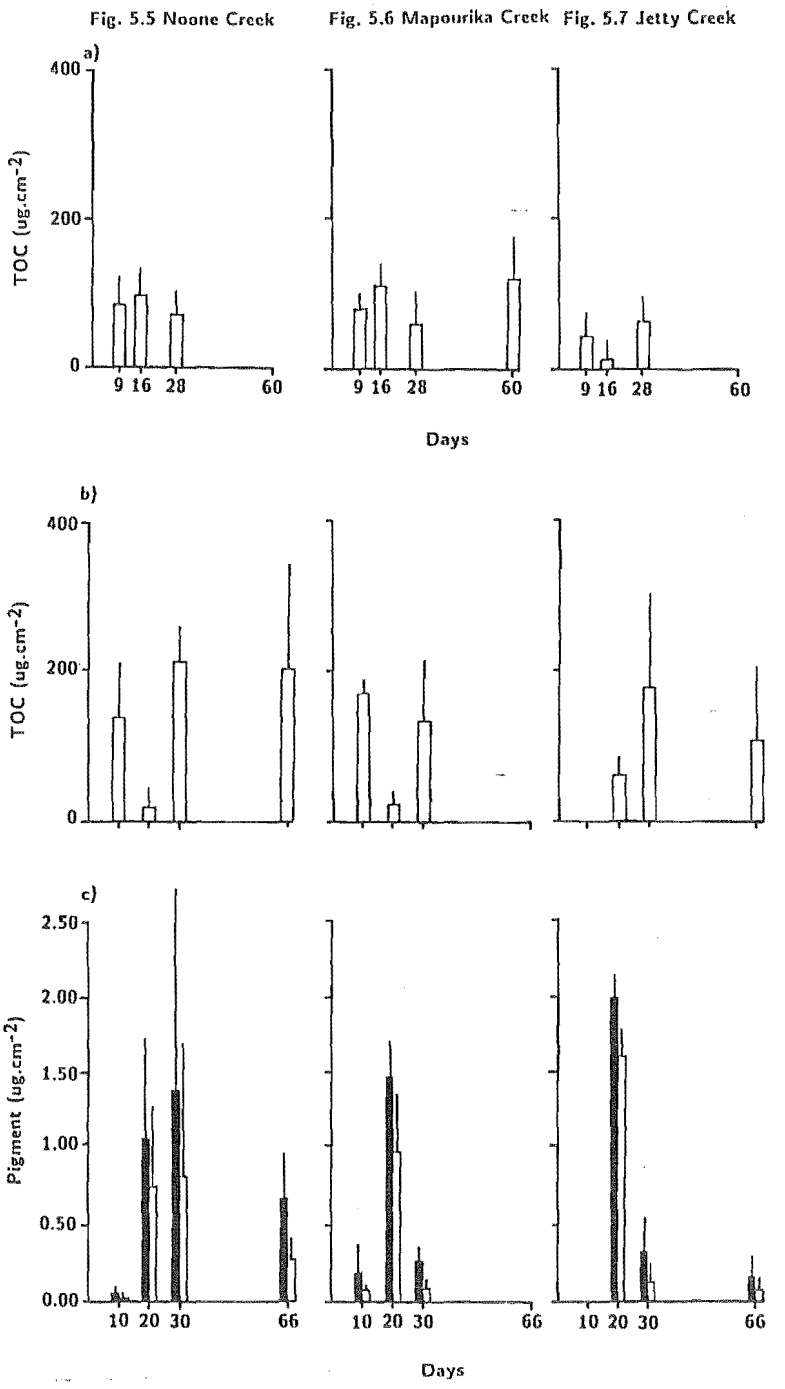
b) Series II

As in Series I, epilithic biomass had developed considerably by day 10, but for an unknown reason a substantial decrease occurred between days 10 and 20 (Fig. 5.5b). Photosynthetic pigment concentrations developed more slowly than TOC and declined between days 30 and 66 (Fig. 5.5c). The colonization pattern observed with SEM was similar to that described for the first incubation series (Plate 5.5). However, after 10 days, species of *Cocconeis* and *Fragilaria* were already colonizing slime covering tile surfaces. Diatom colonization had increased by day 30 when species of *Amphicampa*, *Achnanthes*, *Cymbella*, *Eunotia*, *Fragilaria*, *Frustulia*, *Navicula* and *Surirella* were also common.

(ii) Mapourika Creek

a) Series I

As in Noone Creek, organic carbon concentration on tiles was almost maximal on day 9 after which only minor fluctuations were apparent (Fig. 5.6a). After 9 days the tile surface was covered by an amorphous organic matrix and flocculated organic material, bacterial rods and cocci were visible (Plate 5.6). There was little change in the appearance of the epilithon throughout the remainder of the incubation period, although a few stalked diatoms, *Gomphonema* spp. were seen on day 16 and filaments of an unidentified blue-green alga were present after 28 days.

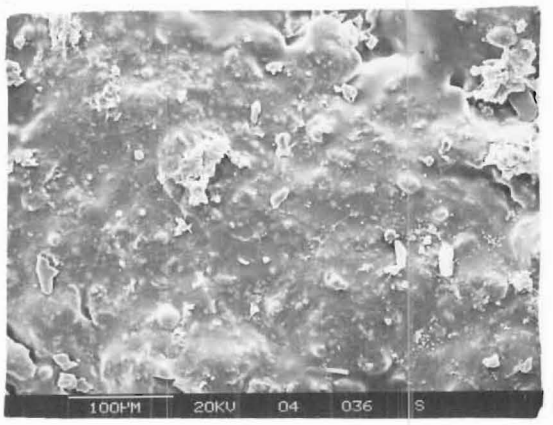



Figures 5.5 - 5.7. Values of epilithic parameters measured on tiles collected after approximately 10, 20, 30, and 60 days incubation in Noone (Fig. 5.5), Mapourika (Fig. 5.6) and Jetty Creeks (Fig. 5.7). For b), X-axis labelling indicated on c).

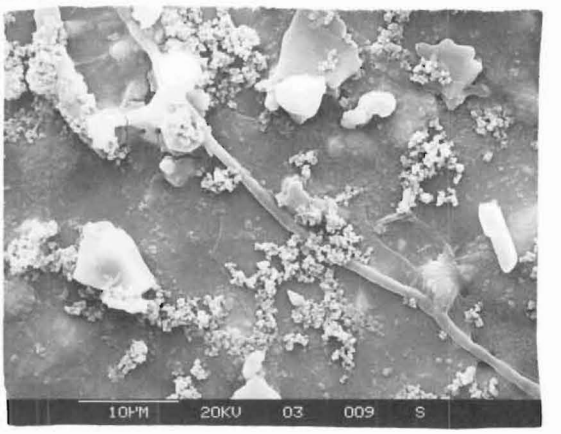
a) Mean TOC concentration (±2SE) on 5 tiles collected between November 1984 and January 1985.
b) Mean TOC concentration (±2SE) on 5 tiles collected between March 1985 and May 1985.
c) Mean concentration (±2SE) of total photosynthetic pigments (shaded histograms) and chlorophyll *a* (open histograms) on 4 tiles collected between March 1985 and May 1985.

**Plate 5.5.** Scanning electron micrographs showing the development of epilithon on the upper surfaces of tiles at Noone Creek during Series I (November-December 1984). After 9 days, tile surfaces were covered with an amorphous slime layer (A) and flocculated organic material (B). By day 16 (C,D), further colonization by bacteria, a few diatoms (*Cocconeis*), blue-green algal spores, and filamentous algae (*?Lyngbya*) was observed. After 28 days (E,F), numerous diatoms (*Surirella* sp.- E, *Eunotia* spp.- E,F, *Taballaria* sp. - E) and filamentous mats were present. Epilithic development was similar in Series II, except that algae colonization was greatest by day 20.

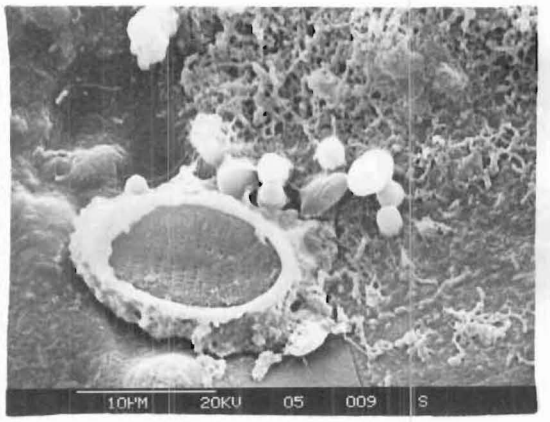
A


100µM 20KV 04 036 S

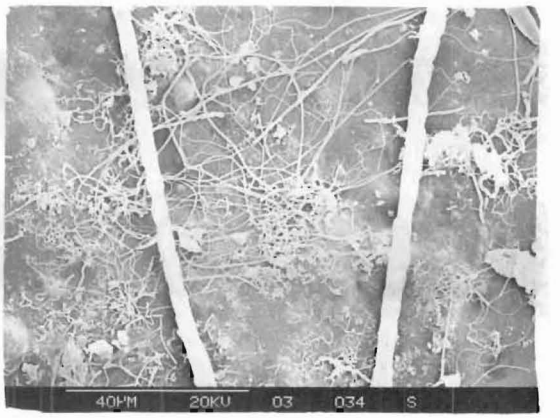
B


10µM 20KV 03 009 S

C


10µM 20KV 05 009 S

D


40µM 20KV 03 034 S

E


100µM 20KV 04 001 S

F

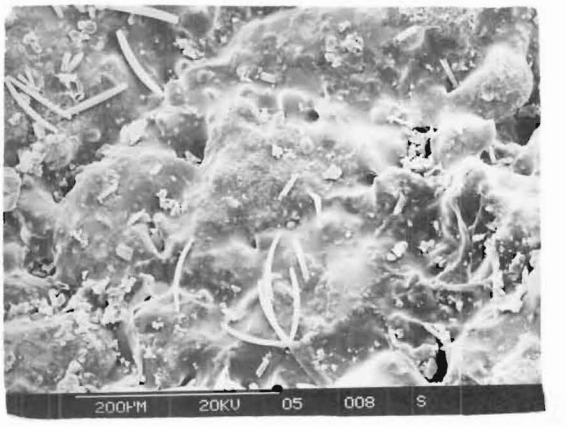
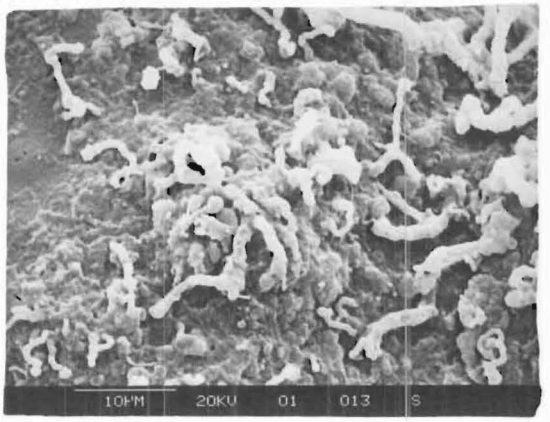
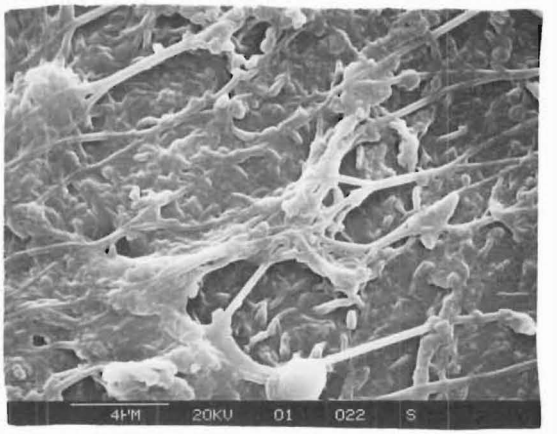

200µM 20KV 05 008 S

**Plate 5.6.** Scanning electron micrographs showing the short-term development of epilithon on the upper surfaces of tiles at Mapourika Creek. Tile surfaces observed during Series I were covered with an amorphous slime layer (A), flocculated organic material (A) and numerous bacteria and Actinomycetes (B) and little change was observed over time. In Series II, however, diatoms - *Cocconeis* (E), *Eunotia* (C,D), *Frustulia* (D), *Fragilaria* and chains of *Tabellaria* (F) were abundant by day 20.

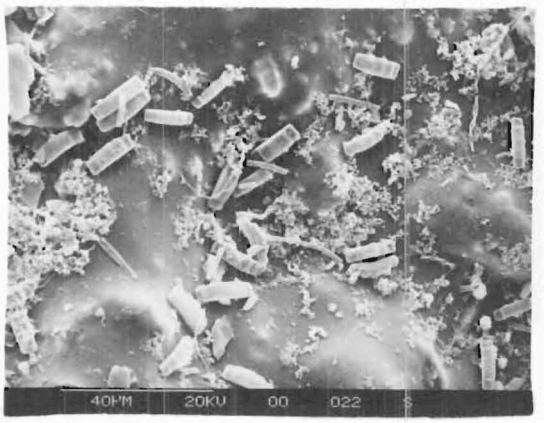
A


10PM 20KV 01 013 S

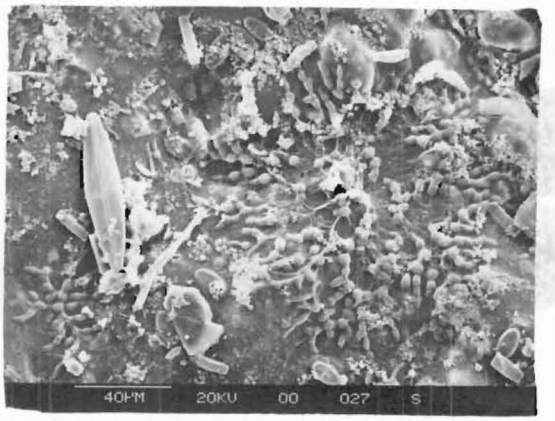
B


4PM 20KV 01 022 S

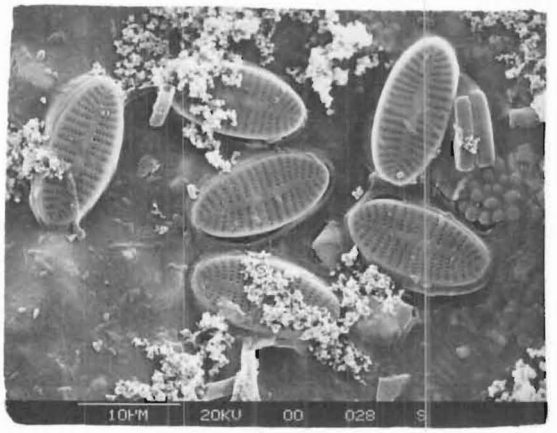
C


40PM 20KV 00 022 S

D


40PM 20KV 00 027 S

E


10PM 20KV 00 028 S

F

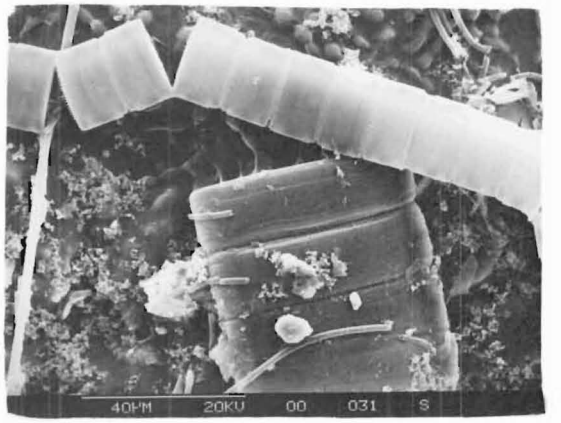
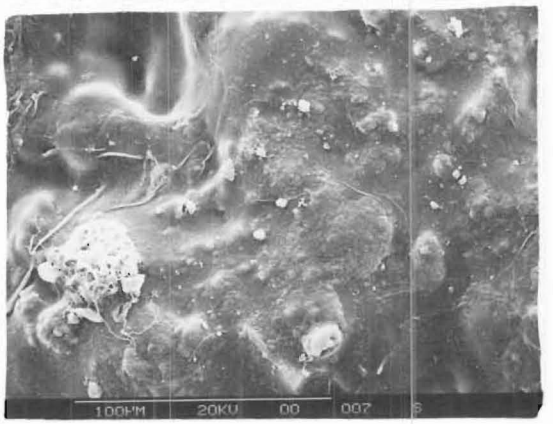
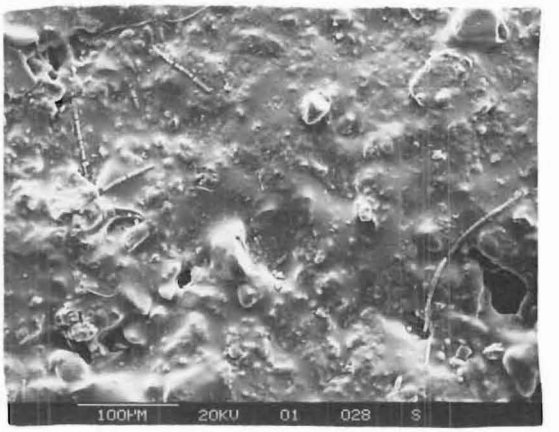

40PM 20KV 00 031 S

**Plate 5.7.** Scanning electron micrographs showing the short-term developing epilithon on the upper surfaces of tiles incubated at Jetty Creek. In both series, tile surfaces were covered with an amorphous slime layer (A,B,C), flocculated organic material (F) and numerous bacteria and fungal filaments (E) and no significant changes in structure were observed. The occasional diatom and filamentous alga were seen after 20 to 30 days incubation (C,D,F).

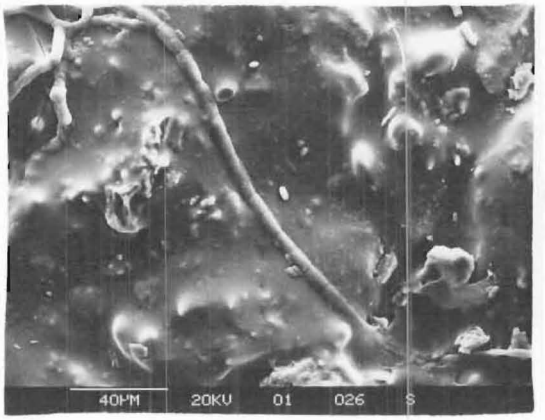
A


100µM 20KV 00 007 S

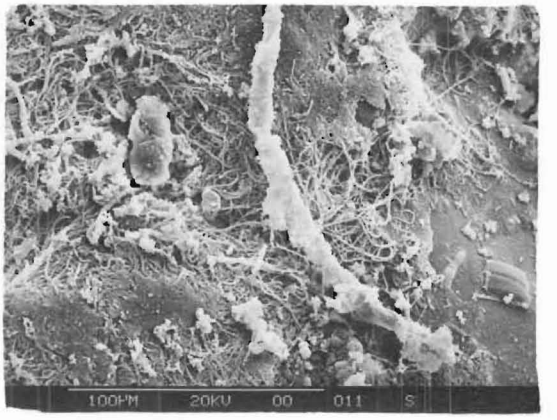
B


100µM 20KV 01 028 S

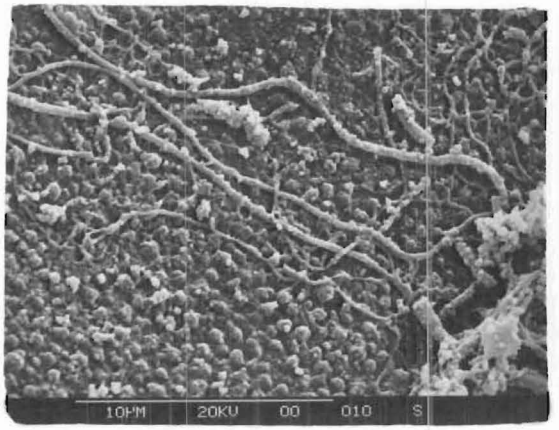
C


40µM 20KV 01 026 S

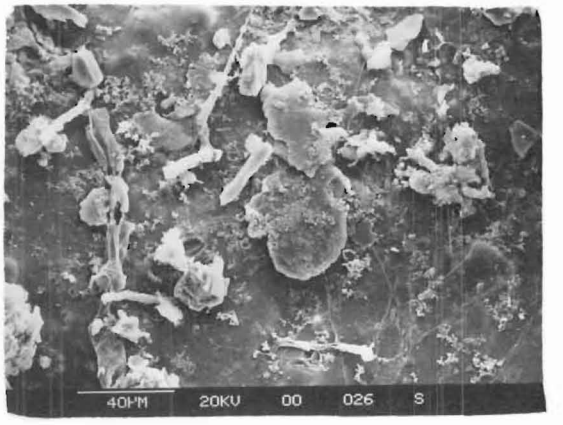
D


100µM 20KV 00 011 S

E


10µM 20KV 00 010 S

F


40µM 20KV 00 026 S

b) Series II

Epilithic carbon concentration was greatest on day 10 (173 ug.cm$^{-2}$) and declined considerably between days 10 and 20 as in Noone Creek (Fig. 5.6b). By day 10, the amorphous organic matrix was heavily colonized by bacterial rods and cocci and *Eunotia*, *Fragilaria* and *Navicula* were present, although not abundant (Plate 5.6). Algal abundance was greatest on day 20, when species of *Cymbella*, *Cocconeis*, *Fragilaria*, and *Coleochaete* were abundant and pigment concentrations were maximal (Fig. 5.6c).

(iii) Jetty Creek

a) Series I

TOC levels showed little change over time and were lowest after 16 days incubation (Fig. 5.7a). By day 9 the surfaces of tiles were covered by an amorphous, organic matrix and both flocculated organic material and unidentified filaments (algal or fungal) had covered this initial matrix by day 16 (Plate 5.7). Bacterial rods and cocci were abundant after 28 days incubation but few diatoms were observed at any time.

b) Series II

Organic carbon content on tiles was greatest after a month and had decreased slightly by day 66 (Fig. 5.7b). In contrast, total pigment concentration was highest on day 20 and then declined markedly (Fig. 5.7c). Electron micrographs showed that on day 20 tile surfaces were covered by an amorphous organic matrix, blue-green algal filaments, *Eunotia* spp. and numerous bacterial rods and cocci (Plate 5.7). However, the major materials and organisms covering tiles collected after 30 and

66 days incubation were flocculated organic material and bacterial rods and cocci.

(iv) Comparison among streams

In the first series (November-January), epilithic standing crops on tiles built up rapidly in all three streams and reached a maximum of about 120 ug $C.cm^{-2}$. Biomass was lowest in Jetty Creek on two of the four dates when direct comparisons could be made.

Higher standing crops were recorded in the second series (March-May) than in the first and may have been a consequence of the lower rainfall recorded during this incubation period (921 mm compared to 1747 mm). In all streams, maximum TOC and pigment concentrations recorded were about 170 and 1.5 $ug.cm^{-2}$, respectively, and occurred during periods of relatively low and stable flows.

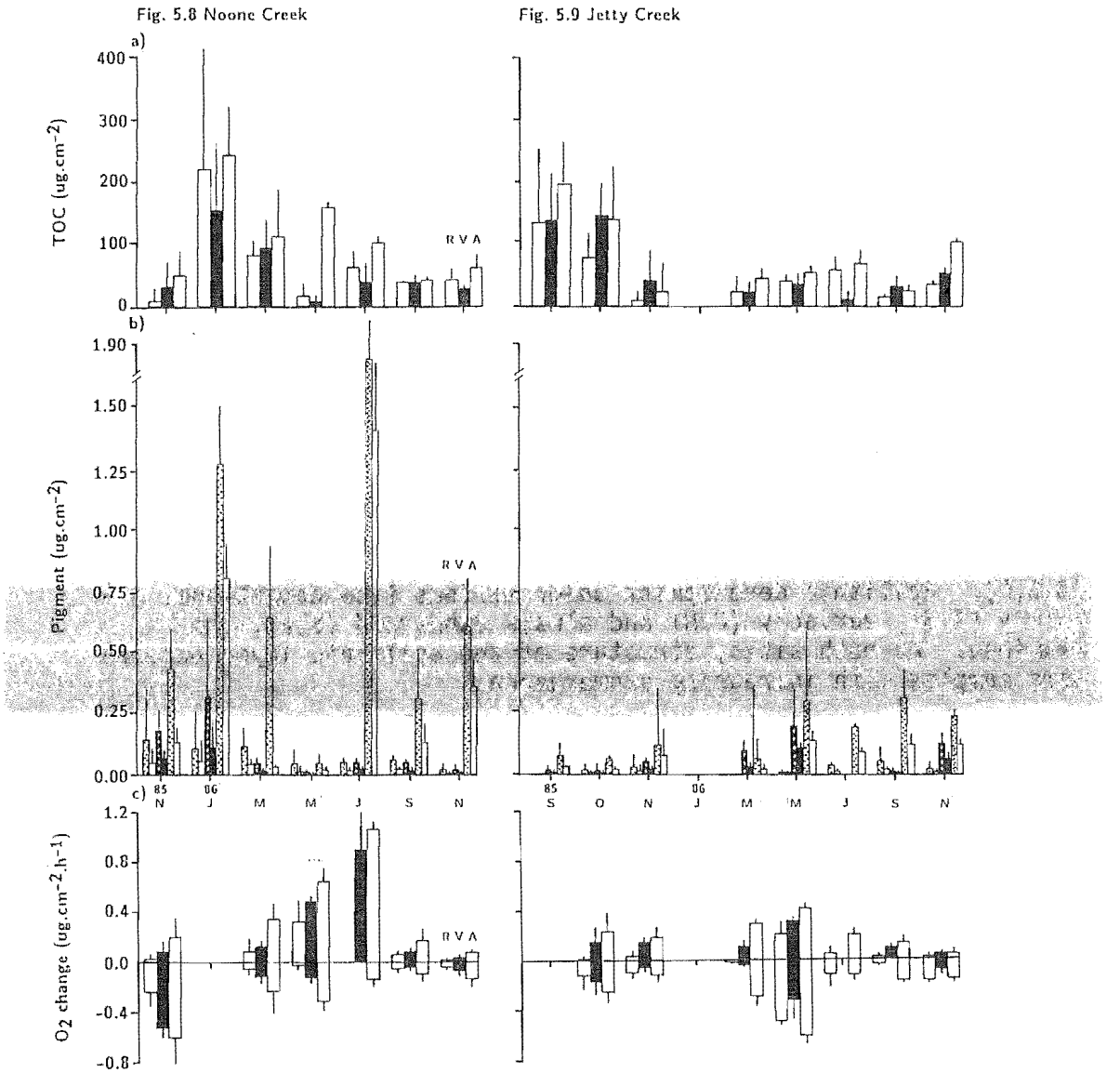
Biological composition of the epilithon differed among streams. Noone Creek had the richest and most complex epilithic layers which included numerous diatom genera (*Amphicampa*, *Achnanthes*, *Cocconeis*, *Cymbella*, *Eunotia*, *Fragilaria*, *Frustulia*, *Navicula* and *Surirella*) as well as filamentous blue-green and green algae and bacteria that colonized the amorphous, surface matrix. Epilithon that developed on tiles at Jetty Creek included few algae (*Eunotia*), but numerous bacterial rods and cocci. At Mapourika Creek the epilithon had an intermediate appearance. The diatoms *Eunotia*, *Fragilaria* and *Navicula*, were patchily distributed, and slime layers were often colonized only by bacterial rods and cocci.

C. Effect of variable flows on epilthon development

The effect of periodic exposure to air on epilithic biomass, primary production and respiration was investigated in the most constant and most variably flowing streams - Noone and Jetty Creeks, respectively. Tiles were placed in 3-tiered substrate holders which held them 0, 10 and 20 cm above the substratum (referred to hereafter as lower, intermediate and upper tiles). Experiments were carried out every 2 months in both streams from November 1985 to November 1986 and in September and October 1985 in Jetty Creek.

(i) Noone Creek

Epilithic standing crops, production and respiration rates are shown in Figure 5.8 a-c. TOC concentrations on lower tiles ranged from slightly greater to 15 times greater than on tiles taken from the intermediate or upper tiles and were notably less variable (Table 5.4). Chlorophyll *a* concentration exhibited a similar pattern to total pigment concentration and was at least eight times higher than on intermediate or upper tiles. Net photosynthetic rates and respiration rates were higher than those on tiles from the other treatments.

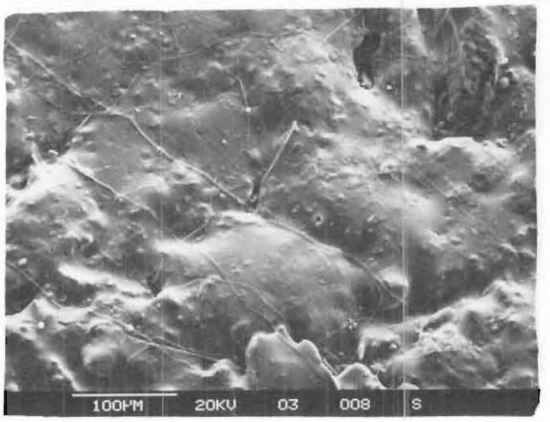



**Figures 5.8, 5.9.** Values of epilithic parameters measured on tiles collected from three submergence regimes: rarely submerged=upper (R - left, open histogram), variably submerged=intermediate (V - shaded histogram) and always submerged=lower tiles (A - right, open histogram), between September 1985 and November 1986 from Noone (Fig. 5.8) and Jetty Creeks (Fig. 5.9). Labelling for all X-axes indicated on b).

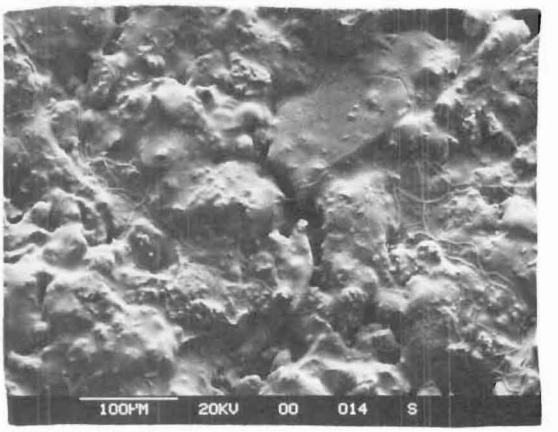
a) Mean TOC concentrations (±2SE) on 5 tiles.
b) Mean concentrations (±2SE) of total photosynthetic pigments (stippled histogram) and chlorophyll *a* (open histogram) on 4 tiles.
c) Mean rates (±2SE) of net $O_2$ evolution and community respiration obtained from 5 tiles incubated under light and dark conditions.

Plate 5.8. Scanning electron micrographs of epilithon colonizing the upper surfaces of tiles at Noone (A,C,E) and Jetty Creeks (B,D,F). Epilithic development under various flow conditions: rarely (upper tiles - A,B), variably (intermediate tiles - C,D) and always submerged (lower tiles - E,F), was examined. At both sites, structure of the epilithic layer became more complex with increasing submergence.

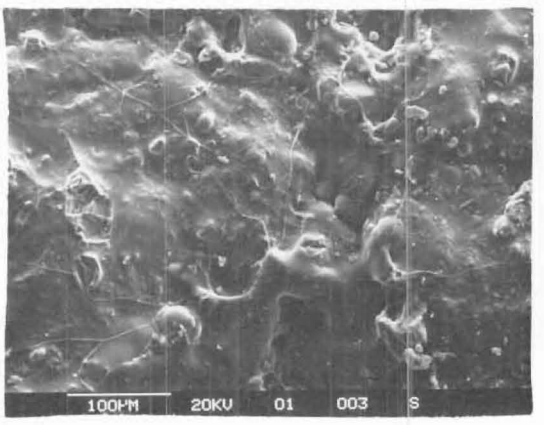
A


100PM 20KV 03 008 S

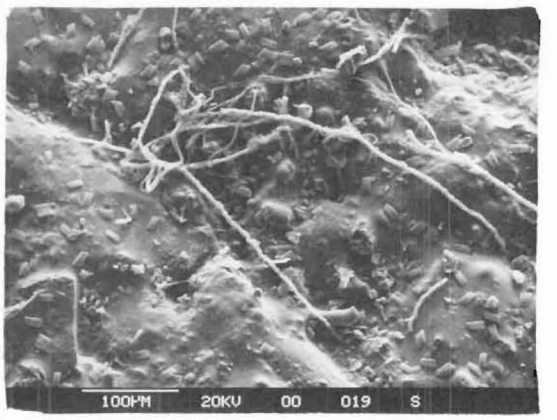
B


100PM 20KV 00 014 S

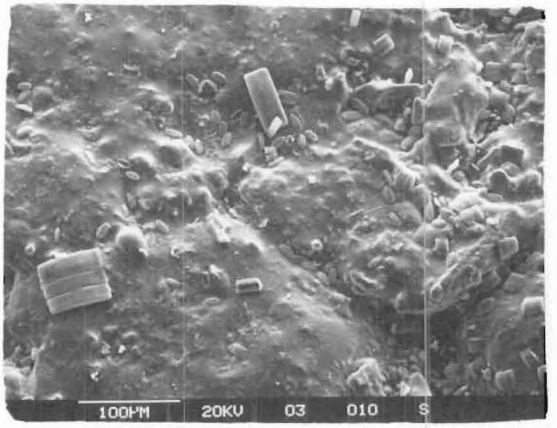
C


100PM 20KV 01 003 S

D


100PM 20KV 00 019 S

E


100PM 20KV 03 010 S

F

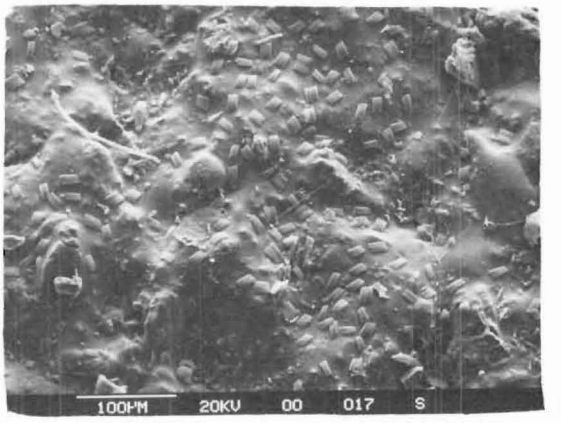

100PM 20KV 00 017 S

Table 5.4. Coefficients of variation for epilithic parameters measured on tiles (n= 5) incubated at Noone Creek under the 3 submergence regimes. Values for 7 trials are shown.

| Regime | Dates | TOC | Tot Pig | Chl a | CR | NCPP |
|---|---|---|---|---|---|---|
| Always submerged tiles | Nov 85 | 78 | 38 | 46 | 27 | 57 |
| | Jan 86 | 36 | 23 | 17 | -- | -- |
| | Mar 86 | 75 | 46 | 14 | 76 | 32 |
| | May 86 | 126 | 81 | 81 | 20 | 15 |
| | Jul 86 | 11 | 45 | 48 | 47 | 3 |
| | Sep 86 | 6 | 58 | 58 | 6 | 58 |
| | Nov 86 | 36 | 29 | 31 | 43 | 26 |
| | x,SE | 52,21 | 70,9 | 42,12 | 36,12 | 32,11 |
| Variably submerged tiles | Nov 85 | 121 | 48 | 43 | 12 | 107 |
| | Jan 86 | 79 | 100 | 108 | -- | -- |
| | Mar 86 | 56 | 31 | 26 | 43 | 35 |
| | May 86 | 86 | 107 | 117 | 36 | 7 |
| | Jul 86 | 81 | 39 | 50 | 0 | 39 |
| | Sep 86 | 26 | 25 | 29 | 27 | 41 |
| | Nov 86 | 22 | 91 | 89 | 51 | 47 |
| | x,SE | 67,17 | 63,17 | 66,18 | 28,9 | 46,17 |
| Rarely submerged tiles | Nov 85 | 170 | 134 | 112 | 48 | 172 |
| | Jan 86 | 98 | 137 | 154 | -- | -- |
| | Mar 86 | 28 | 66 | 56 | 92 | 105 |
| | May 86 | 114 | 104 | 116 | 88 | 50 |
| | Jul 86 | 41 | 42 | 43 | 0 | 0 |
| | Sep 86 | 11 | 35 | 27 | 11 | 47 |
| | Nov 86 | 43 | 114 | 113 | 61 | 100 |
| | x,SE | 72,29 | 90,21 | 89,24 | 50,17 | 79,30 |

(ii) Jetty Creek

TOC concentration on lower tiles was usually about twice that on intermediate or upper tiles (Fig. 5.9a) and showed less temporal variation (Table 5.5). Chlorophyll *a* concentration followed a similar pattern to total pigment concentration and both were at least four times greater on lower tiles than on intermediate or upper tiles, respectively. Net photosynthesis and respiration rates from lower tiles were less variable and twice the rates recorded from intermediate and upper tiles (Figs. 5.9b,c).

Table 5.5. Coefficients of variation of epilithic parameters measured on tiles (n=5) incubated at Jetty Creek under 3 submergence regimes. Values for 8 trials are shown.

| Regime | Dates | TOC | Tot Pig | Chl a | CR | NCPP |
|---|---|---|---|---|---|---|
| Always submerged tiles | Sep 85 | 39 | 59 | 64 | -- | -- |
| | Oct 85 | 67 | 7 | 23 | 40 | 61 |
| | Nov 85 | 154 | 187 | 134 | 59 | 47 |
| | Mar 86 | 41 | 115 | 119 | 32 | 43 |
| | May 86 | 18 | 93 | 96 | 12 | 11 |
| | Jul 86 | 35 | 6 | 13 | 43 | 21 |
| | Sep 86 | 31 | 36 | 43 | 7 | 38 |
| | Nov 86 | 8 | 8 | 8 | 19 | 128 |
| | x,SE | 49,23 | 64,32 | 62,25 | 30,9 | 50,19 |
| Variably submerged tiles | Sep 85 | 61 | 122 | 114 | -- | -- |
| | Oct 85 | 38 | 144 | 137 | 72 | 79 |
| | Nov 85 | 102 | 23 | 28 | 14 | 28 |
| | Mar 86 | 75 | 44 | 34 | 32 | 40 |
| | May 86 | 45 | 74 | 95 | 49 | 5 |
| | Jul 86 | 92 | -- | -- | -- | -- |
| | Sep 86 | 57 | 141 | 142 | 0 | 16 |
| | Nov 86 | 16 | 24 | 23 | 65 | 32 |
| | x,SE | 61,14 | 81,27 | 82,26 | 39,14 | 33,13 |
| Rarely submerged tiles | Sep 85 | 97 | 0 | 0 | - | - |
| | Oct 85 | 56 | 137 | 143 | 106 | 200 |
| | Nov 85 | 150 | 127 | 125 | 47 | 115 |
| | Mar 86 | 100 | 0 | 0 | 113 | 200 |
| | May 86 | 25 | 98 | 100 | 7 | 39 |
| | Jul 86 | 36 | 14 | 13 | 84 | 93 |
| | Sep 86 | 18 | 105 | 115 | 38 | 100 |
| | Nov 86 | 9 | 150 | 144 | 28 | 80 |
| | x,SE | 61,25 | 79,32 | 80,32 | 60,21 | 118,31 |

(iii) Comparison between streams

In both streams, measures of epilithic standing crop, net primary production and respiration were higher and varied less as the amount of aerial exposure declined. Exposure to air clearly inhibited the development of stone surface organic layers (Plate 5.8). Epilithic carbon concentration on lower tiles was similar in both streams and generally about twice that of intermediate or upper tiles. However,

pigment concentrations on tiles from the lower level were almost three times greater in Noone Creek than Jetty Creek. The higher algal biomass of Noone Creek was reflected in greater net photosynthetic rates which on average were about twice those recorded from Jetty Creek. Epilithic respiration rates were similar in both streams, however, pointing to the presence of a greater heterotrophic population in Jetty Creek despite the more open stream channel.

D. Effects of invertebrate grazing on epilithic biomass

The effect of invertebrate grazing on epilithic biomass was investigated in the stream with the lowest variation in flow continuity and the highest benthic densities of invertebrate grazers - Noone Creek. Results of three 2-month long trials using ridged red-brick tiles are shown in Figure 5.10.

On all sampling occasions, epilithic biomass on "ungrazed" substrata was significantly higher than on surfaces exposed to "normal grazing pressures" (Plate 5.9, Kruskal Wallis statistic 5.5, 6.1 & 10.4; $p < 0.01$, 0.05 & 0.01; df 19, 9 & 17, respectively) and was on average 3.6 times greater than on the "grazed" treatment. These results indicate that invertebrate grazers are able to reduce epilithic biomass in Noone Creek.

Contrary to the findings of Cooper & Dudley (1988), the petroleum jelly "barrier" around the edges of the tiles was found to be effective for excluding many invertebrates from upper tile surfaces. Invertebrates on the surfaces of both "grazed" and "ungrazed" tiles were counted prior to tile collection in September and November 1986 and on each occasion, their numbers were significantly lower on the tiles with the barrier

(invertebrate numbers on "grazed" and "ungrazed" tiles: 15, 3; Wilcoxon signed rank test: 3.28 (September) and 1.97 (November), n= 16, 29, $p < 0.05$).

**Plate 5.9.** Photograph showing the accumulated epilithon on two ridged red-brick tiles joined along their longitudinal edge; one with ("ungrazed" - LHS) and one without petroleum jelly barriers ("grazed" - RHS).

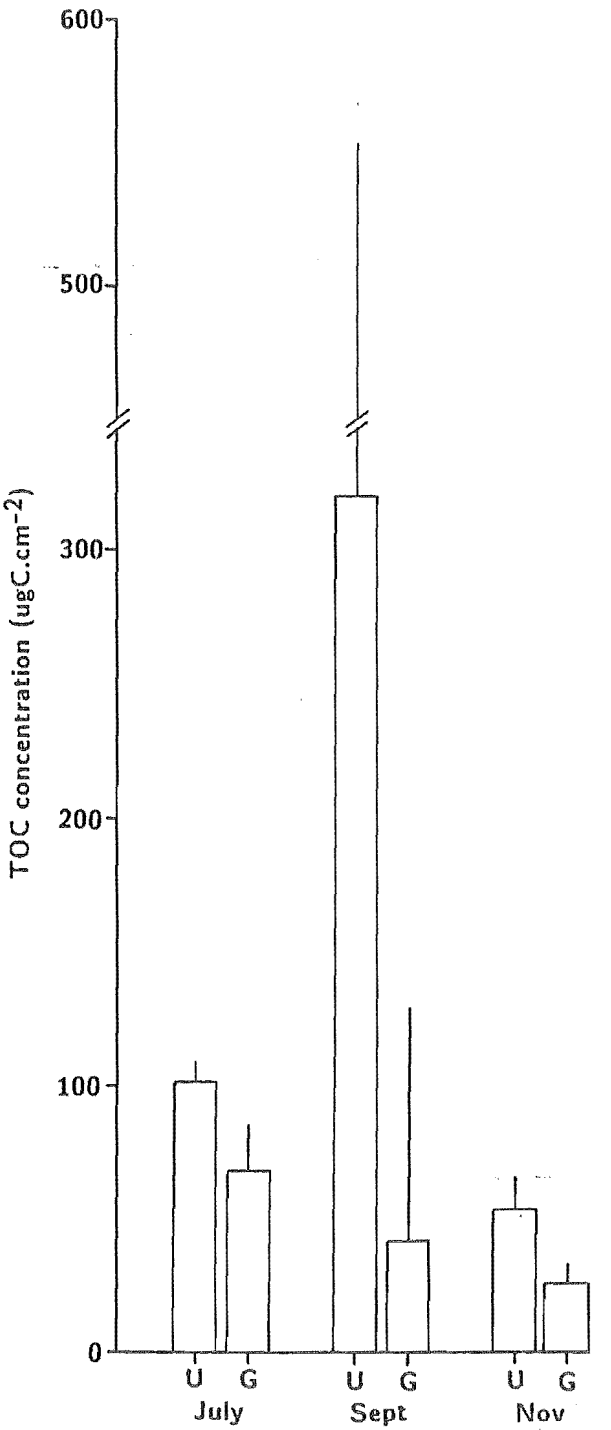



Figure 5.10. Mean TOC concentrations (±2SE) on 6 ridged, red-brick tiles with (U) and without (G) a petroleum jelly barrier to exclude invertebrate grazers. Results of 3 2-month trials ending in July, September and November 1986 are shown.

E. Summary

Overall mean epilithic biomasses were low in all four brownwater streams (range 64-111 ug.cm$^{-2}$) and no significant differences in TOC were found among sites. Ratios of GPP:TOC and CR:TOC were low, indicating that a relatively large component of the epilithon had little biological activity.

Short term studies of epilithic development showed that TOC concentrations built up rapidly whereas algal colonization occurred more slowly. Initially, the stone surface layers appeared to be composed of an amorphous slime matrix, which was first colonized by bacteria and aquatic fungi, and later by diatoms and filamentous green and blue-green algae. Biological composition of the epilithon was richest and most complex at Noone Creek, poorest at Jetty Creek and intermediate at Mapourika and Steep Creeks. Floral composition of layers in each stream showed little variation throughout the study period, and no seasonal patterns were evident. However, marked fluctuations in diatom abundances were observed.

Observations made over a 12-month period indicated that recent flow conditions influenced the accumulation of organic material on tiles. TOC was negatively correlated with rainfall recorded within the week prior to sampling and exposure of stone surfaces to air was shown to inhibit the development of epilithon. The frequent occurrence of high flows may be largely responsible for maintaining low epilithic biomass in these streams. However, invertebrate grazing and nitrogen limitation (Winterbourn *et al.* 1988) have also been shown to influence epilithic biomass in these South Westland streams.

F. Stored Detritus

Measures of detritus stored in the streambed were obtained from Surber samples taken from the four streams between January 1985 and May 1986; sampling was continued at Noone Creek until November 1986. Detritus associated with cobbles, and particulate organic matter (POM) in drift samples (transported detritus) were also collected during this period.

(i) Noone Creek (Fig. 5.11a, 5.12a)

Mean amounts of detritus collected in Surber and cobble samples ranged from 7.0 to 59.1 g AFDW.$m^{-2}$ and 5.7 to 16.7 g AFDW.$m^{-2}$ (stone-surface area), respectively. Despite marked temporal fluctuations, detritus values showed no seasonal patterns and were not correlated significantly with any measured physiographic parameters (Table 5.6).

Detritus taken in drift samples ranged from 0 to 4.6 g AFDW.$100m^{-3}$ and increased as rainfall, discharge and water velocity increased (Table 5.6).

(ii) Mapourika Creek (Fig. 15.11b, 5.12b)

As at Noone Creek, no seasonal patterns in the quantity of detritus present in Surber ($\bar{x}$= 15.68, range 4.4-40.1 g AFDW.$m^{-2}$) and cobble ($\bar{x}$= 6.96, range 3.3-10.5 g AFDW.$m^{-2}$) samples were apparent, and no significant correlations were found with any physiographic parameters (Table 5.6).

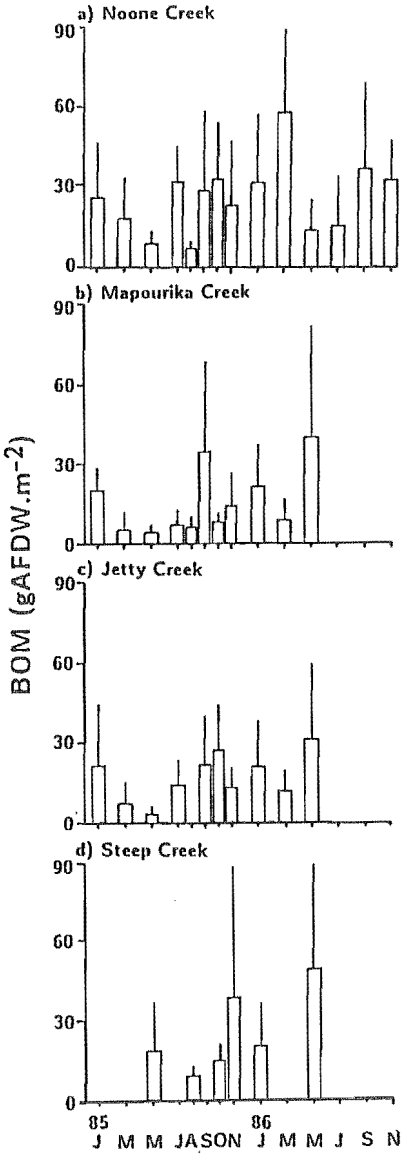



Figure 5.11. Estimates of benthic organic material (x ±2SE) present within the streambeds of a) Noone, b) Mapourika, c) Jetty and d) Steep Creeks, January 1985 - November 1986.

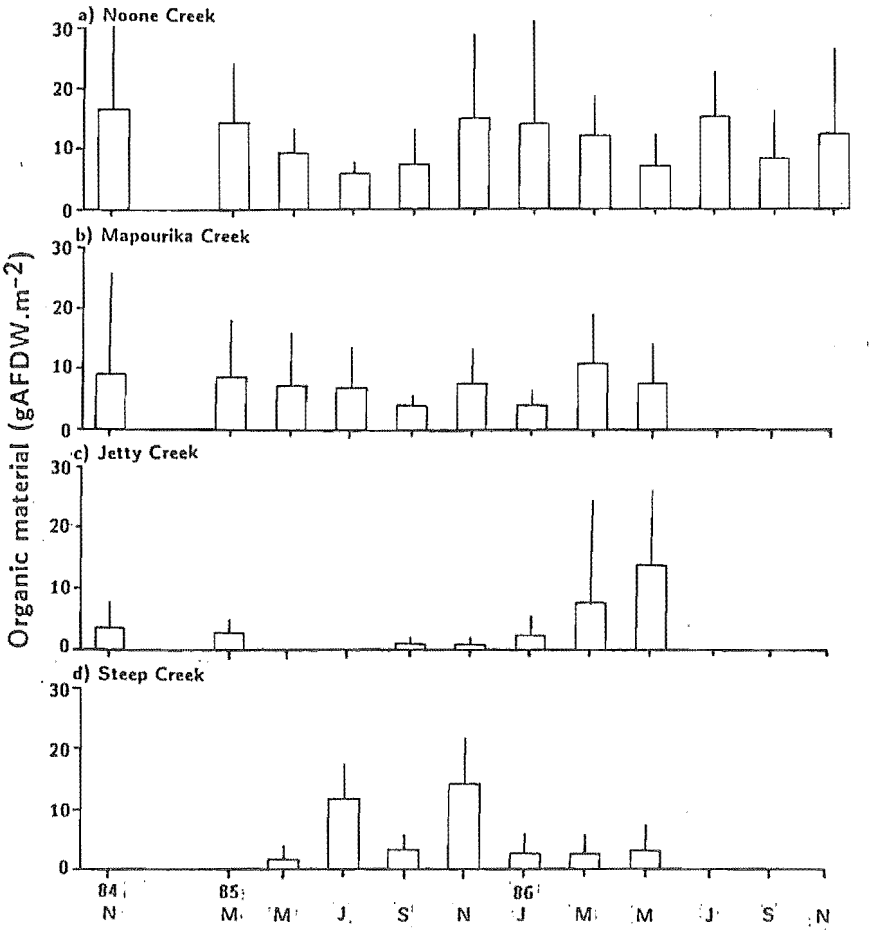



Figure 5.12. Estimates of organic material (x ±2SE) associated with cobbles sampled in a) Noone, b) Mapourika, c) Jetty and d) Steep Creeks (November 1984 -November 1986).

"Monthly" measures of transported detritus ranged from 0 to 0.7 g AFDW.100m$^{-3}$ and were positively correlated with recent flow parameters (Table 5.6).

Table 5.6. Spearman rank correlation coefficients between selected physiographic parameters and mean "monthly" values of a) detritus in Surber samples, b) detritus in cobble samples and c) detritus in drift samples collected at the four streams. For all combinations, * and ** denote $p< 0.05$ and $p< 0.01$, respectively. ND indicates that no samples were collected.

| Sites: | Noone | Mapourika | Jetty | Steep |
|---|---|---|---|---|
| a) Detritus in the Surber samples | n=14 | n=11 | n=10 | n=6 |
| Rainfall during previous week | -0.331 | 0.025 | -0.036 | -0.143 |
| Discharge at time of sampling | -0.237 | 0.104 | -0.054 | -0.086 |
| Water velocity at time of sampling | -0.329 | 0.045 | 0.032 | -0.106 |
| b) Detritus in cobble samples | n=12 | n=9 | n=7 | n=7 |
| Rainfall during previous week | 0.439 | 0.583 | 0.643 | -0.589 |
| Discharge at time of sampling | 0.339 | 0.033 | 0.214 | -0.625 |
| Water velocity at time of sampling | 0.295 | 0.059 | -0.025 | 0.550 |
| Water depth at time of sampling | -0.133 | -0.064 | 0.055 | -0.125 |
| Surface area of cobble | -0.284 | 0.365 | 0.172 | 0.354 |
| c) Detritus in drift samples | n=9 | n=8 | n=8 | |
| Rainfall during previous week | 0.863** | 0.810* | 0.857** | ND |
| Discharge at time of sampling | 0.813** | 0.798* | 0.702* | ND |
| Water velocity at time of sampling | 0.824** | 0.768* | 0.754* | ND |

(iii) Jetty Creek (Fig. 5.11c, 5.12c)

Detritus stored within the streambed ranged from 3.5 to 31.4 g AFDW.m$^{-2}$ and that associated with cobbles ranged from 1.3 to 14.3 g AFDW.m$^{-2}$. Spatial variability was so high that no seasonal patterns of abundance were apparent.

POM in drift samples ranged from 0 to 0.2 g AFDW.100m$^{-3}$ and showed no seasonal trends, however mean "monthly" values were positively correlated with all physiographic parameters (Table 5.6).

(iv) Steep Creek (Fig. 5.11d, 5.12d)

Detritus present in Surber and cobble samples ranged from 8.9 to 49.1 g AFDW.$m^{-2}$ and 2.4 to 14.8 g AFDW.$m^{-2}$, respectively and showed again no seasonal patterns. No significant correlations were found with any physiographic parameters measured (Table 5.6).

(v) Comparisons among streams

Despite differences in the physical structure of the four study sites (ie. sediment size, channel slope and presence of instream vegetation and riparian cover), levels of stored detritus were similar in the four streams. At all sites, values of detritus obtained from Surber and cobble samples were ranged between 0 and 60 gAFDW.$m^{-2}$ throughout the study, values that are low on a world-wide scale (Bott *et al.* 1985, Gurtz *et al.* 1988). The spatial distribution of detritus was extremely patchy in all streams.

Physiographic parameters measured on each sampling date were never significantly correlated with any quantitative measures of benthic detritus (Table 5.6). On average, 177 raindays and 5236 mm of rain are recorded each year in this area of South Westland (N.Z. Meteorological Service) and the high frequency and intensity of rainfall appears to result in the continual mobilization of organic material, which is unable to accumulate on the streambed. This contention is supported by the results of drift sampling which showed that concentrations of transported detritus were positively correlated with flow (Table 5.6).

# Chapter Six

# STREAM FAUNAS

## A. Composition of benthic invertebrate assemblages

Eighty-six taxa of invertebrates were identified in benthic samples collected from the four streams between November 1984 and November 1986. Seventy-nine taxa were either larval or adult stages of aquatic insects, and included 18 plecopterans, 14 dipterans, 10 ephemeropterans, 28 trichopterans, 7 coleopterans and 2 other insect taxa (Table 6.1). Non-insect taxa were Hydracarina, Oligochaeta, Gastropoda, Bivalvia, Ostracoda, Amphipoda, and Decapoda.

Although faunal assemblages differed among the streams, 39 taxa were found in all four. Of these, Oligochaeta, *Stenoperla maclellani* (Plec.), *Acroperla trivacuata* (Plec.), *Zelandobius confusus* (Plec.), *Spaniocerca zelandica* (Plec.), *Spaniocercoides* sp. (Plec.), *Deleatidium* spp. (Eph.), *Hydrobiosis* sp. (Trich.), *Psilochorema* sp. (Trich.), *Hydrochorema crassicaudatum* (Trich.), *Hydrobiosella stenocerca* (Trich.), *Zelolessica cheira* (Trich.), Hydraenidae (Coleo.), Eriopterini spp. (Dipt.), Chironomidae (Dipt.), Empididae (Dipt.), Ceratopogonidae (Dipt.), and Hydracarina, were collected from each stream on more than half the sampling occasions.

Composition of the faunal assemblages differed among streams as indicated above. Low numbers of molluscs were collected from Noone and Steep Creeks and ostracods were found only in Jetty and Steep Creeks.

Table 6.1. Invertebrate taxa identified in all samples of invertebrates collected from the 4 streams between November 1984 and November 1986. * = relative abundance > 1% of invertebrates collected; + = present, - = not collected and (#) number of trips when each taxon was recorded in Surber or cobble samples.

| | Noone | | | Mapourika | | | Jetty | | | Steep | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Surber | Cobble | Drift | Surber | Cobble | Drift | Surber | Cobble | Drift | Surber | Cobble |
| Phylum Annelida | | | | | | | | | | | |
| Class Oligochaeta | *(14) | +(7) | * | *(8) | +(1) | * | *(8) | - | * | *(8) | +(3) |
| Phylum Mollusca | | | | | | | | | | | |
| Class Gastropoda | | | | | | | | | | | |
| Potamopyrgus antipodarum | +(1) | +(1) | - | - | - | - | - | - | - | - | - |
| Class Bivalvia | - | - | - | - | - | - | - | - | - | - | - |
| Phylum Arthropoda | | | | | | | | | | | |
| Class Insecta | | | | | | | | | | | |
| Order Collembola | - | - | + | +(1) | - | + | +(1) | - | - | - | - |
| Order Ephemeroptera | | | | | | | | | | | |
| Deleatidium spp. | *(14) | *(11) | * | *(11) | *(9) | * | *(11) | *(6) | * | *(9) | *(7) |
| Austroclima sepia | +(3) | - | - | +(3) | +(1) | - | - | - | - | - | - |
| Mauiulus luma | - | - | + | - | - | - | - | - | - | - | - |
| Zephlebia sp. A | +(1) | - | - | +(1) | - | - | - | - | - | - | - |
| Zephlebia indet. | +(3) | - | + | +(1) | - | - | - | - | - | - | - |
| Coloburiscus humeralis | *(12) | *(7) | * | - | - | - | - | - | - | - | - |
| Nesameletus sp. | +(4) | +(2) | + | +(7) | +(2) | + | +(1) | - | + | - | +(2) |
| Rallidens mcfarlanei | +(1) | - | - | - | - | + | - | - | - | - | - |
| Ameletopsis perscitus | +(2) | +(1) | + | +(2) | +(3) | + | - | - | + | +(9) | +(4) |
| Oniscigaster wakefieldi | +(3) | +(1) | + | - | +(1) | - | - | - | - | - | - |
| Order Plecoptera | | | | | | | | | | | |
| Stenoperla maclellani | +(13) | +(3) | + | +(6) | +(1) | + | *(9) | +(1) | + | *(9) | +(3) |
| Austroperla cyrene | *(13) | +(9) | + | +(9) | +(2) | * | +(2) | - | + | *(8) | +(1) |
| Megaleptoperla diminuta | - | - | - | +(1) | +(2) | - | - | - | - | - | - |
| Acroperla trivacuata | +(4) | +(6) | + | +(4) | +(4) | * | +(5) | +(2) | + | +(4) | +(5) |
| Acroperla sp. | +(4) | +(2) | - | +(3) | - | - | - | - | - | +(3) | +(5) |
| Zelandoperla agnetis | +(1) | +(2) | - | +(1) | +(2) | - | - | - | - | - | - |
| Z.decorata | +(1) | +(1) | + | +(1) | +(1) | + | +(1) | +(1) | + | +(2) | +(1) |
| Z.fenestrata | +(2) | +(2) | - | +(1) | +(1) | - | +(2) | +(2) | - | +(1) | +(1) |
| Zelandoperla indet. | +(4) | +(1) | + | +(4) | +(3) | * | +(2) | - | + | +(1) | +(1) |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Zelandobius confusus | +(5) | +(6) | + | | *(7) | +(4) | * | | *(6) | +(3) | + | | *(5) | +(5) |
| Z.furcillatus | - | +(1) | - | | - | - | - | | +(2) | +(1) | - | | +(3) | - |
| Zelandobius indet. | *(9) | +(5) | * | | +(4) | +(1) | + | | *(4) | +(3) | + | | +(2) | +(1) |
| Spaniocerca longicauda | - | +(1) | + | | +(2) | - | + | | - | - | - | | - | - |
| S.zealandica | +(3) | +(4) | + | | +(6) | +(1) | + | | +(1) | - | + | | +(1) | - |
| Spaniocerca indet. | +(1) | +(1) | + | | +(3) | - | + | | +(3) | - | * | | +(2) | - |
| Spaniocercoides sp. | +(9) | +(3) | + | | +(5) | - | + | | +(5) | - | + | | +(4) | - |
| Cristaperla fimbria | +(3) | +(2) | + | | +(2) | - | + | | +(1) | - | + | | - | - |
| Halticoperla viridans | +(1) | - | - | | +(2) | - | - | | +(1) | - | - | | - | - |
| Order Megaloptera | | | | | | | | | | | | | | |
| Archichauliodes diversus | +(7) | +(6) | - | | - | - | - | | - | - | - | | *(9) | +(3) |
| Order Trichoptera | | | | | | | | | | | | | | |
| Neurochorema confusum | +(1) | - | - | | +(2) | - | - | | +(1) | - | - | | +(1) | - |
| Hydrobiosis parumbripennis | +(1) | +(8) | * | | +(1) | +(3) | * | | - | - | * | | - | +(4) |
| Hydrobiosis sp. | *(9) | +(4) | * | | *(9) | +(1) | + | | +(3) | +(1) | * | | +(6) | - |
| Costachorema sp. | +(3) | +(2) | + | | +(3) | - | * | | +(1) | - | - | | - | - |
| Psilochorema sp. | *(12) | +(4) | + | | +(8) | +(2) | * | | +(3) | - | + | | +(5) | +(1) |
| Hydrochorema crassicaudatum | +(12) | +(1) | + | | +(7) | - | + | | +(6) | - | * | | - | - |
| Tiphobiosis sp. | - | - | - | | - | - | - | | +(1) | - | - | | - | - |
| Polyplectropus sp. | +(1) | +(1) | + | | +(3) | +(1) | - | | +(1) | - | - | | +(4) | - |
| Hydrobiosella stenocerca | +(7) | +(4) | + | | +(6) | +(2) | + | | +(4) | - | + | | +(5) | - |
| Oxyethira albiceps | *(10) | *(9) | * | | +(1) | +(1) | - | | +(4) | +(1) | + | | +(5) | +(2) |
| Paraoxyethira eatoni gp. | +(5) | +(5) | - | | - | - | - | | - | - | - | | +(1) | +(1) |
| Aoteapsyche sp. | +(1) | +(2) | + | | +(1) | - | - | | - | - | - | | - | - |
| Diplectrona sp. | +(2) | +(1) | - | | +(2) | - | + | | - | - | - | | - | - |
| Rakiura vernale | +(1) | *(11) | + | | +(7) | *(8) | + | | - | - | - | | *(7) | +(7) |
| Helicopsyche poutini | *(12) | *(11) | + | | +(8) | *(7) | - | | - | - | - | | - | - |
| Helicopsyche zealandica | +(2) | +(3) | + | | - | +(1) | - | | - | - | - | | - | - |
| Philorheithrus agilis | +(1) | - | - | | - | - | - | | - | - | - | | - | - |
| Hudsonema amabilis | +(3) | +(1) | + | | - | - | - | | - | - | - | | - | - |
| Triplectides sp. | +(7) | +(8) | + | | +(2) | - | + | | - | +(1) | - | | +(4) | +(2) |
| Pycnocentrella eruensis | +(5) | +(2) | - | | +(2) | - | - | | - | - | - | | - | - |
| Zelolessica cheira | *(10) | *(12) | + | | +(6) | *(4) | * | | +(3) | - | + | | *(5) | *(7) |
| Alloecentrella sp. | +(5) | - | + | | +(2) | - | - | | +(2) | - | - | | +(4) | - |
| Conuesucidae indet. | *(7) | +(6) | + | | +(1) | +(4) | + | | - | - | - | | +(1) | - |
| Pycnocentrodes sp. | +(2) | - | - | | +(2) | - | - | | +(1) | - | - | | - | - |
| Conuxia gunni | +(7) | +(3) | + | | +(1) | - | - | | - | - | - | | +(2) | - |
| Olinga feredayi | *(11) | +(3) | + | | +(4) | - | + | | +(1) | - | + | | +(1) | - |
| Pycnocentria funerea | *(9) | +(5) | + | | - | - | - | | - | - | - | | - | +(1) |
| P.evecta | +(1) | +(1) | + | | - | - | - | | - | +(1) | - | | - | - |
| Order Coleoptera | | | | | | | | | | | | | | |
| Staphylinidae (adult) | +(1) | +(1) | * | | +(2) | - | * | | +(1) | - | + | | +(2) | - |
| Hydraenidae (adult) | +(9) | +(6) | + | | +(6) | +(2) | * | | +(5) | - | + | | +(7) | +(3) |
| Hydrophilidae (adult) | | - | + | | +(1) | - | + | | - | - | - | | - | - |
| Hydrophilidae (larvae) | +(5) | +(5) | * | | +(4) | +(2) | * | | +(6) | +(1) | * | | +(3) | +(2) |
| Curculionidae (adult) | +(3) | +(1) | - | | - | - | + | | +(1) | - | - | | +(1) | - |
| Helodidae (larvae) | +(1) | - | + | | *(10) | - | * | | - | +(1) | * | | +(1) | - |
| Elmidae (adult) | +(1) | - | + | | +(4) | - | + | | - | +(1) | + | | - | +(1) |
| Elmidae (larvae) | +(8) | +(1) | + | | +(10) | +(4) | + | | +(1) | - | + | | *(9) | *(7) |
| Ptilodactylidae (larvae) | - | - | + | | - | - | - | | - | - | - | | - | - |
| Order Diptera | | | | | | | | | | | | | | |
| Zelandotipula sp. | +(1) | - | + | | - | - | + | | +(3) | - | - | | - | - |
| Aphrophila neozelandica | *(13) | *(11) | + | | +(4) | +(1) | + | | +(2) | - | - | | - | - |
| Limonia nigrescens | +(4) | +(6) | - | | - | - | + | | +(1) | - | - | | - | - |
| Eriopterini sp. | +(7) | +(5) | + | | +(3) | +(2) | * | | +(8) | - | + | | +(4) | +(1) |
| Hexatomini spp. | - | - | + | | +(1) | +(1) | - | | +(1) | - | - | | +(3) | +(1) |
| Paralimnophila skusei | +(3) | - | - | | - | - | - | | +(1) | - | - | | +(2) | - |
| Austrosimulium spp. | +(1) | - | + | | +(3) | +(3) | + | | +(3) | - | - | | +(5) | +(2) |
| Dixidae | - | - | + | | - | - | - | | - | - | - | | - | - |
| Psychodidae | - | - | - | | +(2) | - | + | | - | - | - | | - | - |
| Chironomidae | *(14) | *(12) | * | | *(11) | *(9) | * | | *(11) | *(7) | * | | *(9) | *(7) |
| Ceratopogonidae | *(9) | +(10) | + | | +(3) | +(2) | - | | +(6) | +(2) | - | | *(9) | +(2) |
| Stratiomyidae | - | - | - | | - | - | + | | - | - | - | | - | - |
| Empididae | +(12) | +(5) | + | | +(5) | +(1) | + | | +(6) | +(1) | + | | *(8) | -(1) |
| Mycetophilidae | +(2) | - | * | | +(1) | - | + | | +(1) | - | + | | - | - |
| Class Crustacea | | | | | | | | | | | | | | |
| Order Ostracoda | +(2) | - | - | | - | - | - | | *(2) | - | - | | *(6) | +(1) |
| Order Amphipoda | +(1) | +(1) | + | | +(2) | +(1) | + | | +(1) | +(1) | + | | +(2) | - |
| Order Decapoda | | | | | | | | | | | | | | |
| Paranephrops planifrons | - | - | - | | - | - | - | | - | - | - | | +(2) | - |
| Class Arachnida | | | | | | | | | | | | | | |
| Order Hydracarina | +(8) | +(5) | + | | +(4) | +(3) | + | | +(2) | +(1) | + | | +(7) | +(3) |

*Coloburiscus humeralis* (Eph.) was taken only in Noone Creek and *Zephlebia* sp. (Eph.) and *Austroclima* sp. (Eph.) only from Noone and Mapourika Creeks.

Tipulid, hydroptilid and conoesucid larvae were most abundant in Noone Creek, but occurred also at the other streams. Helicopsychid larvae (Trich.) were never found in Jetty Creek.

Of the 86 taxa found in benthic samples during the course of the study, 76 were taken from Noone Creek, 54 from Mapourika Creek, 50 from Jetty Creek and 48 from Steep Creek. Overall, numbers of invertebrate taxa (or taxon richness) were significantly different among the streams (Table 6.2). On most sampling occasions, most taxa were recorded at Noone Creek and fewest at Jetty and Steep Creeks.

**Table 6.2.** Results of Friedman's 2-way non-parametric ANOVA on the number of invertebrate taxa recorded in Surber samples collected from a) all 4 study streams (May 1985 - May 1986) and b) Noone, Mapourika and Jetty Creeks (January 1985 - May 1986).

| Comparison | $X_2$ value | df | p |
|---|---|---|---|
| (a) 4 streams (May 1985 - May 1986) | 26.52 | 3 | $p< 0.01$ |
| (b) 3 streams (Jan 1985 - May 1986) | 20.17 | 2 | $p< 0.01$ |

Numerically important taxa, ie. those with relative abundances greater than 1 percent of invertebrates collected in all Surber samples from each of the four streams, are listed in Table 6.3. Chironomidae, *Deleatidium*, Oligochaeta and *Z. confusus* had relative abundances greater than 1 percent in all four streams. *Deleatidium* spp. and chironomid larvae formed 58-77 percent of the invertebrates collected at all sites.

Note that both these groups were composite taxa; no attempt was made to identify chironomid larvae many of which are undescribed Orthocladiinae and species of *Deleatidium* are morphologically similar and cannot be identified.

Figure 6.1 summarizes the number of taxa and their allocation within orders at the four stream sites. Although these graphs do not consider individual species, they demonstrate the high degree of similarity of the faunas at the four sites.

In Noone Creek, 15 taxa had overall relative abundances greater than 1 percent of the total fauna and together comprised 89 percent of the invertebrates collected in Surber samples (Table 6.3). Similarly, at Steep Creek 15 major (> 1%) taxa made up 93 percent of the fauna. At Mapourika and Jetty Creeks only eight and seven major taxa accounted for 84 and 89 percent of the fauna, respectively (Table 6.3).

At Noone Creek, the 15 dominant taxa included Oligochaeta, 7 Trichoptera, 3 Diptera, 2 Ephemeroptera and 2 Plecoptera, whereas at Steep Creek, 3 Diptera and 4 Plecoptera but only 2 Trichoptera and 1 ephemeropteran were included among the 15 dominants (Table 6.3). Five insect orders and the Oligochaeta were represented in the 8 major taxa at Mapourika Creek, whereas the top seven taxa at Jetty Creek belonged to Diptera, Ephemeroptera, Plecoptera, Ostracoda and Oligochaeta. Beetle larvae were common in two streams, Mapourika Creek (Helodidae) and Steep Creek (Elmidae and Hydraenidae), and although commonly found at the two low pH sites (Jetty and Steep Creeks) ostracods were never recorded from Mapourika Creek, the least acidic site.

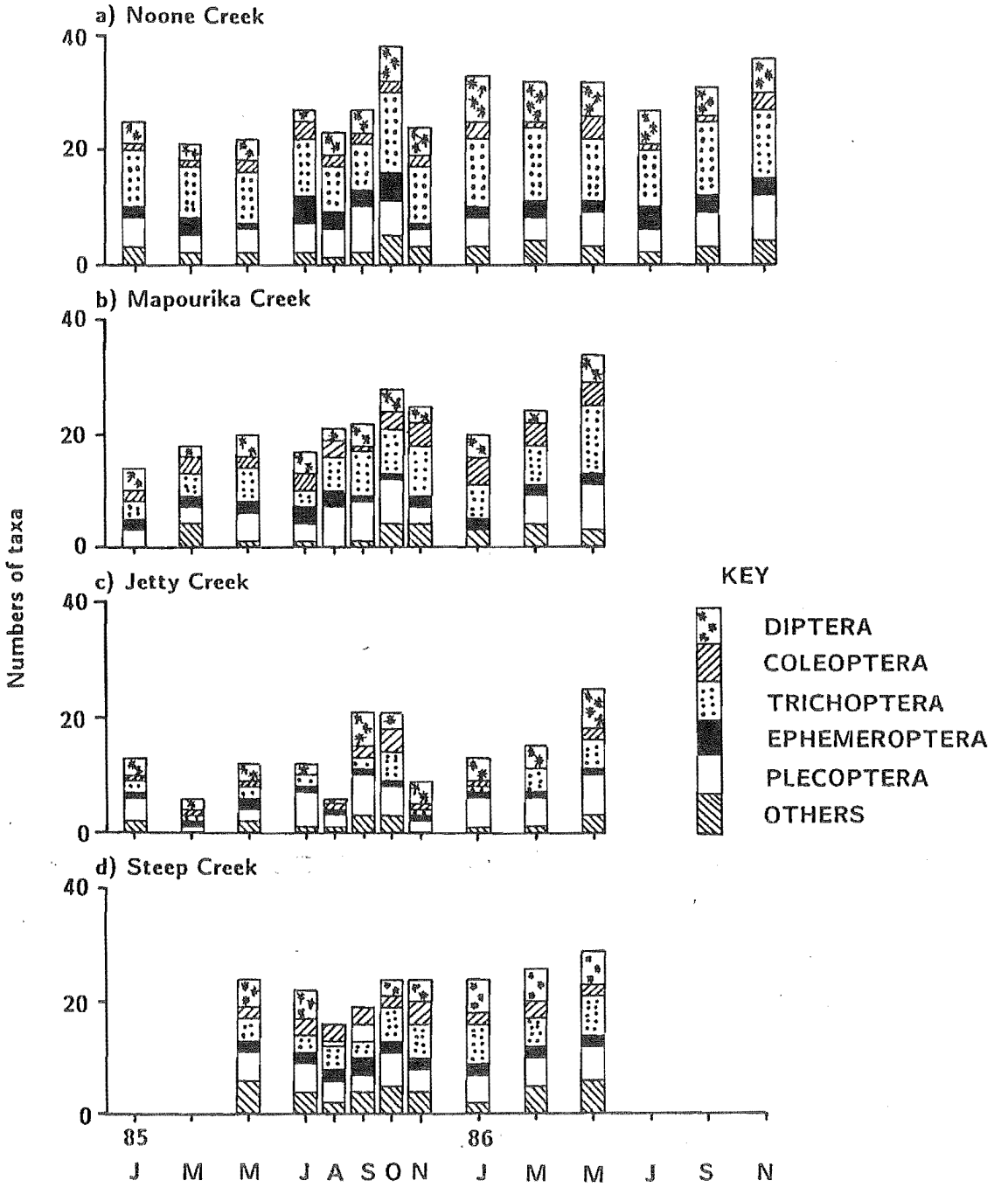



Figure 6.1. Numbers of taxa and their allocation within five major aquatic insect orders (and "others") recorded in benthic samples between November 1984 and November 1986 from a) Noone, b) Mapourika, c) Jetty and d) Steep Creeks.

Table 6.3. Invertebrate taxa with relative abundances greater than 1% of all invertebrates collected in Surber samples listed in order of decreasing abundance. Mean densities ($No.m^{-2}$), coefficents of variation (%) and ranges (in parentheses; $No.m^{-2}$) are given for each major taxon and total benthos. n= Number of collections (ie. sampling dates).

| Noone Creek (n=14) | Mapourika Ck. (n=11) | Jetty Creek (n=11) | Steep Creek (n=9) |
|---|---|---|---|
| Chironomidae | Chironomidae | Chironomidae | *Deleatidium* |
| 436, 64% | 188, 83% | 187, 98% | 382, 75% |
| (132-1062) | (28-548) | (16-552) | (36-1054) |
| *Deleatidium* | *Deleatidium* | *Deleatidium* | Chironomidae |
| 243, 40% | 167, 74% | 165, 67% | 307, 96% |
| (100-442) | (28-392) | (40-400) | (26-822) |
| *P.funerea* | *Z.confusus* | *Z.confusus* | *Z.cheira* |
| 50, 66% | 17, 96% | 27, 57% | 104, 57% |
| (0-120) | (0-44) | (4-54) | (30-206) |
| *Z.cheira* | Helodidae | Oligochaeta | Elmidae |
| 37, 62% | 12, 130% | 8, 121% | 94, 54% |
| (4-70) | (0-48) | (0-34) | (24-198) |
| *A.neozelandica* | *Hydrobiosis* sp. | *S.maclellani* | *Z.confusus* |
| 36, 88% | 8, 124% | 5, 73% | 54, 55% |
| (0-90) | (0-38) | (0-10) | (14-96) |
| *C.humeralis* | Oligochaeta | *A.trivacuata* | Oligochaeta |
| 33, 100% | 6, 112% | 2, 122% | 45, 103% |
| (0-120) | (0-18) | (0-5) | (0-134) |
| *H.poutini* | *Z.cheira* | Ostracoda | *S.maclellani* |
| 33, 78% | 6, 79% | 1, 150 | 20, 51% |
| (6-70) | (0-14) | (0-16) | (8-36) |
| *Z.confusus* | *H.poutini* | | Empididae |
| 31, 98% | 5, 122% | | 17, 68% |
| (2-96) | (0-16) | | (0-36) |
| Oligochaeta | | | Ostracoda |
| 22, 148% | | | 14, 222% |
| (2-134) | | | (0-94) |
| *O.albiceps* | | | *A.trivacuata* |
| 18, 108% | | | 15, 183% |
| (0-72) | | | (0-86) 183% |
| *A.cyrene* | | | Ceratopogonidae |
| 17, 68% | | | 13, 77% |
| (0-38) | | | (2-34) |
| *Hydrobiosis* sp. | | | *A.diversus* |
| 16, 83% | | | 13, 54% |
| (0-52) | | | (2-20) |
| *Psilochorema* sp. | | | Hydraenidae |
| 13, 87% | | | 13, 152% |
| (0-36) | | | (0-52) |
| *O.feredayi* | | | *R.vernale* |
| 13, 116% | | | 13, 155% |
| (0-46) | | | (0-62) |
| Ceratopogonidae | | | *A.cyrene* |
| 12, 126% | | | 12, 120% |
| (0-52) | | | (1-44) |
| Total benthic invertebrate fauna: | | | |
| 1142, 37% | 506, 62% | 450, 73% | 1185, 55% |
| (646-2106) | (146-1198) | (75-1086) | (338-2188) |

Hydrobiosid larvae were the dominant invertebrate predators at Noone and Mapourika Creeks, whereas at Jetty and Steep Creeks, the stonefly *S. maclellani* was the most common invertebrate predator. The predatory megalopteran *Archichauliodes diversus* was frequently collected at Steep Creek, but was rare in the other streams.

B. Densities of benthic invertebrates

(i) Noone Creek

Temporal changes in densities of the total benthic invertebrate fauna and the two major taxa - Chironomidae and *Deleatidium*, between January 1985 and November 1986, are shown in Figure 6.2 a-c. Mean "monthly" densities of benthic invertebrates ranged from 646 to 2106 $m^{-2}$ (x= 1142 $m^{-2}$, CV= 37%, n= 14) and were greatest in September 1986 and lowest in November 1985. Although no seasonal patterns in abundance were apparent, benthic densities recorded during the first year of sampling (January 1985 -January 1986) were slightly but not significantly ($p > 0.05$) lower than those recorded during the second year (January - November 1986).

Chironomid densities ranged from 132 to 1062 $m^{-2}$ (CV= 64%, n=14) and were lowest in May 1985 and highest in September 1986. Although densities were greater in 1986 than 1985, no seasonal patterns were apparent. Overall, temporal changes in chironomid densities in this stream followed a similar pattern to those of the total fauna.

Numbers of *Deleatidium* ranged from 100 to 442 $m^{-2}$ and showed moderate variation over time (CV= 40%, n=14). Maximum densities were recorded during July and September 1985, and September 1986.

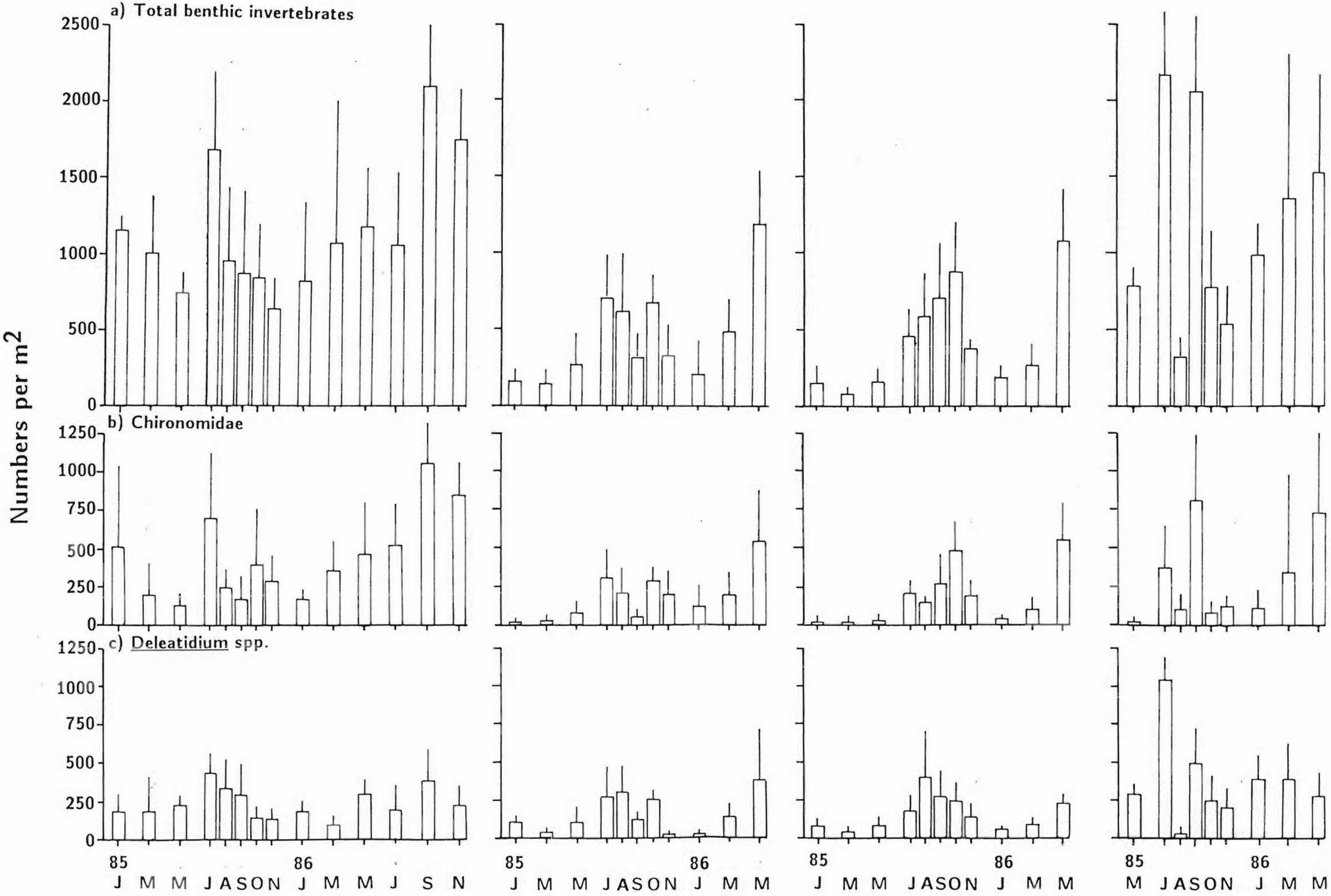
**Figures 6.2-6.5.** Temporal changes in densities (x ±2SE) of a) total benthic invertebrate fauna, b) Chironomidae and c) *Deleatidium* spp. between January 1985 and November 1986 at Noone (Fig. 6.2), Mapourika (Fig. 6.3), Jetty (Fig. 6.4) and Steep Creeks (Fig. 6.5). Labelling for all X-axes indicated on c).

Fig. 6.2 Noone Creek

Fig. 6.3 Mapourika Creek

Fig. 6.4 Jetty Creek

Fig. 6.5 Steep Creek



In general, the mean densities of the other 13 common taxa except *Z. confusus*, were greater in 1986 than 1985, although there was marked temporal variation indicated by high coefficents of variation (CV). Greatest densities of *Z. cheira*, *Aphrophila neozelandica* and *Olinga feredayi* occurred during summer and were in the range 0 to 90 $m^{-2}$ (Table 6.3). Similarly, numbers of *Pycnocentria funerea* and *Z. confusus* were in the range 0 to 120 $m^{-2}$ (Table 6.3), but were highest in winter. The remaining seven taxa - Oligochaeta, *A. cyrene*, *C. humeralis*, *Helicopsyche poutini*, *Oxyethira albiceps*, *Psilochorema* sp., and Ceratopogonidae, had no seasonal patterns of abundance, and in all cases densities were in the range 0 to 134 $m^{-2}$ (Table 6.3).

(ii) Mapourika Creek

Temporal changes in densities of the total benthic invertebrate fauna, *Deleatidium* and Chironomidae, are shown in Figure 6.3 a-c. Mean densities of the fauna ranged from 146 to 1198 $m^{-2}$ ($x$= 506 $m^{-2}$, CV= 62%, n= 14) and were greatest during late winter 1985 (July, August and September) and in May 1986. Densities were lowest in January and March 1985.

Density of the *Deleatidium* population ranged from 28 to 392 $m^{-2}$ (CV= 74%, n= 11) and was greatest in July and August 1985 and May 1986 and lowest in November 1985 and January 1986. *Deleatidium* abundance was greatest therefore during winter as at Noone Creek.

Mean numbers of Chironomidae ranged from 28 to 548 $m^{-2}$ (CV= 83%, n=11), and showed no seasonal pattern of abundance. The other six major taxa, *Z. confusus*, Helodidae, *Hydrobiosis* sp., Oligochaeta, *Z. cheira* and *H. poutini*, all ranged in density from 0 to 48 $m^{-2}$ (Table 6.3) and showed no seasonal abundance patterns.

(iii) Jetty Creek

Temporal changes in densities of the total benthic invertebrate fauna, Chironomidae and *Deleatidium*,are shown in Figure 6.4 a-c. Mean density of the fauna ranged from 75 to 1086 $m^{-2}$ (x= 450 $m^{-2}$, CV= 73%, n= 11), and was temporally more variable than in the other streams.

In different months, densities of Chironomidae and *Deleatidium*, the two most common taxa, ranged from 16 to 552 $m^{-2}$ (CV= 98%, n= 11) and 40 to 400 $m^{-2}$ (CV= 67%, n= 11), respectively and exhibited no clear seasonal patterns of abundance. Neither did *Z. confusus*, Oligochaeta, *S. maclellani*, *A. trivacuata* or Ostracoda, the other five common taxa collected in this stream (Table 6.3).

(iv) Steep Creek

The mean density of the invertebrate fauna in Steep Creek was comparable to that in Noone Creek and about twice that at Mapourika and Jetty Creeks. Again, no clear seasonal patterns of abundance were apparent (Fig. 6.5a).

Mean monthly densities of Chironomidae and *Deleatidium* (Fig. 6.5 b,c) ranged from 26 to 822 $m^{-2}$ (CV= 96%, n= 9) and 36 to 1054 $m^{-2}$ (CV= 75%, n= 9), respectively. Temporal variation was high and masked any possible seasonal patterns in densities. This was also true of the other 13 common taxa, where temporal variation in abundances was particularly marked for Ostracoda (CV= 222%), *A. trivacuata* (CV= 183%), *Rakiura vernale* (CV= 155%), Hydraenidae (CV= 152%), *A. cyrene* (CV= 120%) and Oligochaeta (CV=103%) (Table 6.3).

C. Drift fauna and the fauna colonizing cobbles

Collections of invertebrates were made from cobbles and the water column (drift samples) every two months between November 1984 and May 1986 (November 1984 - November 1986 - Noone Creek only). Cobble sampling was carried out to determine whether the invertebrate assemblage of this particular micro-habitat differed from the general bottom fauna as assessed by Surber and kick sampling. Drift sampling was undertaken to monitor downstream movement of invertebrates at different times of year and under a range of flow conditions. In terms of overall species composition, the fauna collected in the four types of samples (Surber, cobble, kick and drift) in each stream were qualitatively different (Table 6.4).

**Table 6.4.** Qualitative comparisons of faunal composition among sample types using Cochran's Q test (presence/absence data) from a) Noone, b) Mapourika, c) Jetty and d) Steep Creeks. $H_0$: probability of each taxon being present was similar among sample types (Surber, cobble, drift and kick samples).

| Comparison | Q statistic | df | p | $H_0$: |
|---|---|---|---|---|
| a) Noone Ck. | 18.5 | 3 | < 0.01 | reject |
| b) Mapourika Ck. | 20.8 | 3 | < 0.01 | reject |
| c) Jetty Ck. | 24.5 | 3 | < 0.01 | reject |
| d) Steep Ck. | 35.5 | 2 | < 0.01 | reject |

(a) Fauna on cobbles

Five samples of invertebrates and the organic debris associated with cobbles were collected from the four sites every two months from November 1984 to May 1986 (November 1984 - November 1986 at Noone Creek only). Fewer taxa were recorded (64) than in Surber samples (86), and most (56) were rare (either present in numbers less than 1 percent of the total

number of invertebrates on cobbles, or infrequently taken; Table 6.1). On most sampling occasions, the number of taxa recorded from cobble samples was highest at Noone Creek (mean number of taxa per sampling date= 20; overall number of taxa= 60), lowest at Jetty Creek (mean= 5; total= 20) and intermediate at Mapourika and Steep Creeks (mean= 11 and 13; total= 40 and 33, respectively).

Table 6.5. Invertebrate taxa with relative abundances greater than 1% of all invertebrates collected in cobble samples listed in order of decreasing abundance. Mean density, coefficients of variation (%) and ranges (in parentheses; No.$m^{-2}$) are given for each major taxon and total invertebrate density on cobbles. Total taxon richness is given for each site. n= number of collections (ie. sampling dates).

| Noone Creek (n=12) | Mapourika Ck. (n=9) | Jetty Creek (n=7) | Steep Creek (n=7) |
|---|---|---|---|
| Chironomidae<br>289, 60%<br>(107-671) | Chironomidae<br>157, 88%<br>(8-319) | Chironomidae<br>64, 84%<br>(18-163) | *Z. cheira*<br>140, 76%<br>(56-362) |
| *H. poutini*<br>80, 74%<br>(0-181) | *Deleatidium*<br>45,57%<br>(13-95) | *Deleatidium*<br>30, 114%<br>(0-100) | *Deleatidium*<br>70, 28%<br>(56-362) |
| *Z. cheira*<br>50, 85%<br>(5-137) | *H. poutini*<br>18, 123%<br>(0-74) | | Elmidae<br>51,36%<br>(20-73) |
| *C. humeralis*<br>42, 159%<br>(0-181) | *Z. cheira*<br>11, 199%<br>(0-65) | | Chironomidae<br>44, 113%<br>(5-152) |
| *Deleatidium*<br>40, 58%<br>(0-79) | *R. vernale*<br>11, 112%<br>(0-32) | | *R. vernale*<br>24, 72%<br>(3-55) |
| *R. vernale*<br>37, 57%<br>(0-73) | | | |
| *A. neozelandica*<br>33, 92%<br>(0-95) | | | |
| Total invertebrate density on cobbles (No.$m^{-2}$): | | | |
| 767, 35%<br>(367-1202) | 289, 58%<br>(110-595) | 123, 62%<br>(38-225) | 359, 45%<br>(217-641) |
| Total number of taxa recorded: | | | |
| 60 | 40 | 20 | 33 |

Table 6.6. Spearman rank correlation coefficents ($r_s$) between selected biological and environmental parameters associated with individual cobbles sampled in the four streams. For all combinations, * denotes $p < 0.05$ .

| | Total invert. density (No.$m^{-2}$) | Surface area ($m^{-2}$) | Assoc. organic matter | Water velocity | Water depth |
|---|---|---|---|---|---|
| (i) Noone Creek (# cobbles= 60) | | | | | |
| Taxon richness | 0.767* | 0.255* | 0.351* | 0.046 | -0.011 |
| Total density | 1.000 | 0.259* | 0.263* | -0.196 | 0.063 |
| *Deleatidium* | 0.484* | 0.273* | 0.204 | 0.223 | -0.127 |
| *C. humeralis* | 0.467* | 0.193 | 0.293 | 0.064 | -0.159 |
| *R. vernale* | 0.059 | 0.117 | 0.257* | 0.096 | 0.152 |
| *H. poutini* | 0.517* | 0.222 | 0.260* | 0.141 | -0.045 |
| *Z. cheira* | 0.204 | 0.073 | 0.295* | 0.533* | 0.056 |
| *A. neozelandica* | 0.303* | 0.293* | 0.143 | -0.034 | 0.016 |
| Chironomidae | 0.805* | 0.170 | 0.191 | -0.387* | 0.232 |
| (ii) Mapourika Creek (# cobbles= 45) | | | | | |
| Taxon richness | 0.748* | 0.285* | 0.365* | 0.175 | -0.024 |
| Total density | 1.000 | 0.383* | 0.233 | 0.074 | -0.056 |
| *Deleatidium* | 0.378* | 0.272* | 0.336* | 0.432* | -0.057 |
| Chironomidae | 0.716* | 0.332* | 0.215 | 0.075 | 0.064 |
| *H. poutini* | 0.115 | 0.280* | 0.092 | 0.005 | 0.007 |
| *Z. cheira* | 0.566* | 0.435* | 0.319* | 0.023 | 0.038 |
| *R. vernale* | 0.104 | 0.177 | 0.160 | 0.163 | 0.098 |
| (iii) Jetty Creek (# cobbles= 35) | | | | | |
| Taxon richness | 0.812* | 0.084 | 0.447* | -0.125 | 0.205 |
| Total density | 1.000 | 0.512 | 0.343* | -0.057 | 0.117 |
| *Deleatidium* | 0.674* | 0.512 | 0.343 | 0.108 | 0.078 |
| Chironomidae | 0.849* | 0.242 | 0.197 | -0.100 | -0.075 |
| (iv) Steep Creek (# cobbles= 35) | | | | | |
| Taxon richness | 0.772* | 0.363* | 0.354* | -0.025 | 0.067 |
| Total numbers | 1.000 | 0.431* | 0.400* | 0.005 | 0.038 |
| *Deleatidium* | 0.391* | 0.131 | -0.163 | 0.045 | 0.173 |
| Chironomidae | 0.608* | 0.112 | 0.335 | 0.073 | -0.059 |
| *Z. cheira* | 0.859* | 0.470* | 0.468* | 0.525* | 0.025 |
| Elmidae | 0.762* | 0.373* | 0.304 | 0.023 | -0.056 |

Seven major taxa comprised between 80 and 90 percent of the invertebrates collected from cobbles at each site (Table 6.5). They were *Deleatidium*, *C. humeralis*, *R. vernale*, *H. poutini*, *Z. cheira*, Elmidae, Chironomidae and *A. neozelandica*. Only *Deleatidium* and Chironomidae were common on cobbles at Jetty Creek (84 % of fauna) where trichopterans were rare. Larvae of the tipulid, *A. neozelandica* and the siphlonurid mayfly, *C. humeralis* were only common on cobbles at Noone Creek, whereas elmid larvae were abundant at Steep Creek.

Correlations between selected biological and environmental parameters associated with cobbles sampled at each site are shown in Table 6.6. At all sites, the strongest (or one of the strongest) positive correlations was between the total density of invertebrates and taxonomic richness. Both these biological parameters were positively correlated with surface area of cobble and with the mass of detritus associated with each cobble. However, they were never significantly correlated with water velocity or water depth taken at the time of sampling. Similar correlations were also obtained for most major taxa at each site (Table 6.6), indicating that cobble dwellers tolerate a wide range of flow conditions.

(b) Drift fauna (see also Appendix Two)

Drifting invertebrates and suspended particulate organic matter were collected from three streams (Noone, Mapourika and Jetty Creeks) every two months from November 1984 to March 1986. Sampling was undertaken simultaneously at the three sites with nets being emptied before sunset and after sunrise on two consecutive days.

Invertebrate taxa taken in drift samples are shown in Table 6.1. Composition of the drift was similar at the three sites from which 34 (Jetty), 48 (Mapourika) and 54 (Noone) aquatic taxa were taken.

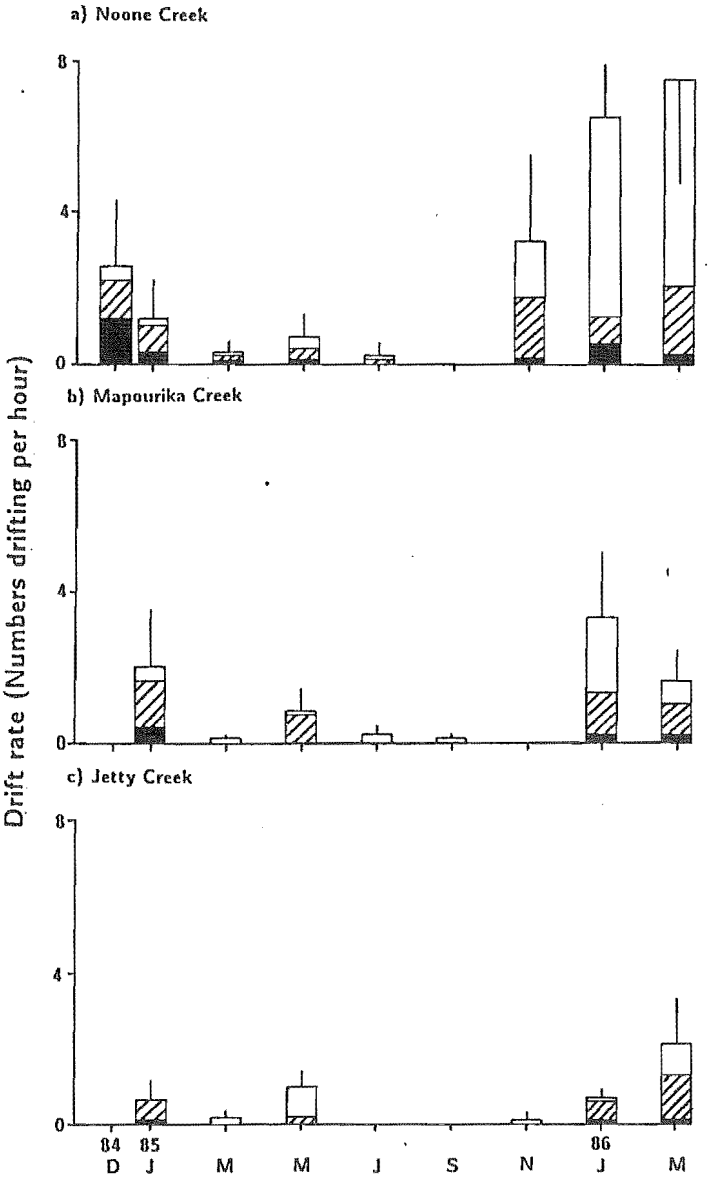



Figure 6.6. Drift rates (numbers of invertebrates collected per unit time) of the total fauna (aquatic and terrestrial - unshaded; x ±2SE), aquatic invertebrates (hatched) and *Deleatidium* (shaded) recorded during nine sampling periods from a) Noone, b) Mapourika and c) Jetty Creeks. Labelling for all X-axes indicated on c).

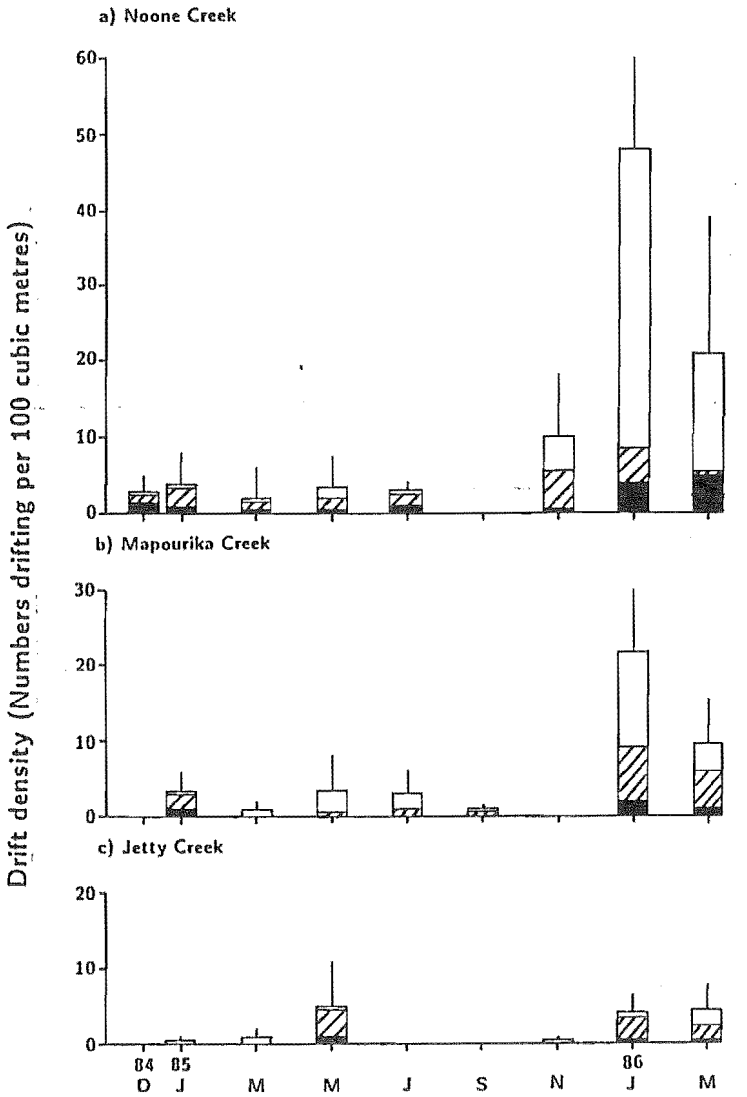



Figure 6.7. Drift densities (numbers of invertebrates collected per volume unit of water filtered) of the total fauna (aquatic and terrestrial - unshaded; x ±2SE), aquatic invertebrates hatched) and *Deleatidium* (shaded) recorded during nine sampling periods from a) Noone, b) Mapourika and c) Jetty Creeks. Labelling for all X-axes indicated on c).

Terrestrial species including the adult stages of some aquatic invertebrates were a major component of the drift at all sites. The most abundant terrestrial groups were Collembola, Arachnida, Diptera and Hymenoptera.

*Deleatidium* nymphs, and larval Chironomidae were the most abundant aquatic invertebrates taken in drift; larvae of *Hydrobiosis*, *Psilochorema* and *Zelandobius* species, Oligochaeta and a hydrophilid beetle were also common. At Noone Creek, *C.humeralis*, *Z.confusus*, *O.albiceps*, *Z.cheira* and Mycetophilidae larvae also made up more than 1% of total invertebrates collected.

Figures 6.6 and 6.7 show drift rates and densities of the total fauna (including terrestrial invertebrates), aquatic invertebrates and *Deleatidium* nymphs taken during the nine sampling periods. Drift rates (numbers of invertebrates collected per unit time, ie. uncorrected for discharge) were highest at Noone Creek and lowest at Jetty Creek, site differences that were consistent over time (Friedman's nonparametric 2-way ANOVA $X^2$= 23.45, 17.39, k= 3, n= 9, $p < 0.01$). However, site differences were not found when drift densities (or numbers of aquatic organisms in drift samples per $100m^3$ per h) were compared.

As no differences in drift density were found among sites, data were pooled from the three sites to compare densities of aquatic invertebrates during day and night periods. More aquatic invertebrates, especially *Deleatidium* nymphs were drifting at night than during the day (Wilcoxon matched pairs test: Z= -4.28, -3.22, n= 60, $p < 0.01$). Night drift densities of aquatic invertebrates and *Deleatidium* were markedly greater (2.5 and 4 times, respectively) than day drift densities.

Although rates and densities of drifting aquatic organisms ranged from 0 to 2 invertebrates per hour and 0 to 10 invertebrates per $100m^3$,

respectively, over the period of study, no seasonal patterns were apparent. Instead, temporal differences appeared to be more strongly influenced by flow conditions immediately before and at the time of sampling. Thus, a significant positive correlation was found between numbers of drifting invertebrates and discharge (day $r_s$= 0.56; night $r_s$= 0.75, n=60, p< 0.01). However, drift density was negatively correlated with discharge (day $r_s$= -0.37, night $r_s$= -0.56, n=60, p< 0.01).

Interpretation of these results is not easy without knowledge of the effect of flow on the distances drifted by benthic invertebrates, as this determines the effective area of benthos being sampled. If drift distances do not vary with discharge, then an increase in numbers of invertebrates in the drift can be taken to indicate "catastrophic drift". If drift distance is directly related to water velocity as found by Elliott (1971) for some Northern Hemisphere mayfly species and other aquatic insects, then drift density may be a better measure with which to assess the drift response of benthic invertebrates to changes in flow. If so, then the decreasing drift densities found in this study as discharge increased could be interpreted to mean that invertebrates actively avoided entering the water column at such times, perhaps by going deeper into the substratum. Further work on drift distances of benthic invertebrates under varying flow conditions is necessary to validate this hypothesis.

D. Variation in benthic invertebrate assemblages among streams

A fundamental problem in sampling stream invertebrate assemblages is to obtain adequate and representative estimates of the numbers of all invertebrate taxa within the streambed. The sampling program should be such that the underlying distributions of taxa are effectively sampled, but this is always limited by the number of samples that can be collected and processed. In my study, five benthic samples were taken with a Surber sampler from each stream on each sampling occasion, and the sampling effort was comparable among the four streams.

The range of habitats sampled within each stream was necessarily restricted by the type of sampler employed as well as by the number of samples collected. According to the Surber data obtained, taxa such as *C. humeralis* and *Zelandoperla* sp., were rare at most sites, but they were collected more frequently when other sampling methods were used. This indicates that their particular micro-habitats within the streambed were not adequately sampled using the Surber sampler. Taxa with specialized habitat requirements (eg. loosely compacted fine sediments beneath large stones, spray zones on large boulders) were therefore under-collected.

Benthic invertebrate assemblages were compared among streams using two non-parametric statistical procedures, Cochran's Q test and Kendall's coefficent of concordance (W), to identify patterns in taxon occurrence.

a) Cochran's Q test

This test compares the observed variance in total numbers of taxa among sites with the variance expected under the null hypothesis ($H_0$) that "r" taxa are independently distributed among "n" sites, when the data are dichotomized ordinal information, ie. a taxon is either present

or absent at each site (Siegel 1956). Data are arranged in a presence/absence matrix of "n" columns and "r" rows, where "n" is the number of sites and "r" is the total number of taxa recorded.

Significant values of Q were obtained when the total faunal assemblages of the four streams were compared ($Q= 42.5$, $p< 0.01$), but a difference in faunal composition was not found when only the major taxa were included in the comparison (Table 6.7). The faunal assemblages of the four streams comprised a small set of dominant taxa and a large collection of rarer taxa. The presence/absence of "rare" taxa influenced the statistical procedure more than the dominant taxa, when total fauna was used to calculate Q, as all taxa have equal weighting.

Table 6.7. Comparisons of faunal composition (presence/absence) among streams using Cochran's Q test a) all taxa and b) major taxa (as in Table 6.3) in Surber samples. $H_0$: probability of taxon being present was similar among sites. $p< 0.01$ indicates that faunal composition differed significantly among sites).

| | Q | df | p | $H_0$ |
|---|---|---|---|---|
| a) All taxa | 42.5 | 3 | < 0.01 | reject $H_0$ |
| b) Major taxa | 10.8 | 3 | > 0.05 | accept $H_0$ |

Twenty-four of the 87 taxa taken in Surber samples were categorized as "dominants" in one or more of the streams. Although rare taxa were expected to occur, it was surprising to find that over two thirds of them were "rare", that is, comprised less than 1 percent of the total numbers of invertebrates collected in Surber samples. Twenty-one of the 87 taxa recorded were collected on less than 3 sampling occasions and another 34 taxa were taken at only one or two sites. Because Surber sampling was confined to flowing waters with gravel and cobble substrates, some of

these "rare" taxa could have been more abundant in other habitats, or they may have been truely rare.

b) Kendall's coefficient of concordance

Kendall's coefficent of concordance (W), a statistic obtained by a multiple rank correlation procedure (Siegel 1956), was used to measure the degree of association among the four sites with respect to the ranked abundances of their major taxa (data from all months were totalled and ranked). The null hypothesis tested was that abundance rankings were randomly distributed among taxa. As ranked abundances were used in the analysis, the procedure was not influenced by differences in densities among sites.

**Table 6.8.** An assessment of among stream variation in faunal composition using Kendall's coefficent of concordance (W) for a) major taxa (relative abundance greater than 1%) in Surber samples and, b) major taxa except *Deleatidium* and Chironomidae. $H_0$: rankings of abundances of major taxa differed among sites. $p < 0.01$ indicates that the rankings of each taxon were similar among streams.

| | W | df | p | $H_0$ |
|---|---|---|---|---|
| a) 24 taxa | 0.51 | 23 | < 0.01 | reject $H_0$ |
| b) 22 taxa | 0.35 | 21 | < 0.01 | reject $H_0$ |

Statistically significant differences in faunal compositions of the four streams were not found (Table 6.8), when Kendall's W was used to make comparisons among sites. This was so when all 24 dominant taxa were included in the comparisons and when *Deleatidium* and Chironomidae, the two most abundant taxa, were omitted. In both cases, significant agreement in abundance rankings of taxa existed among the streams and implied that the faunal assemblages of the four streams were

fundamentally similar. This was despite many taxa being rarely collected, and absolute densities differing among the streams.

When all 87 taxa were included in the comparisons, the Q statistic indicated that faunal assemblages of the four streams differed significantly, whereas Kendall's W indicated that there were no site differences in major components of the faunal assemblages. Although the results of the two tests are contradictory, they highlight several interesting features of the fauna. Thus, it is clear that the faunas had a small group of dominant taxa that were abundant in all four streams.

Rare taxa created a large matrix and since all taxa are given equal weight when calculating Cochran's Q, the statistic was almost certainly over-influenced by the presence or absence of rare species whose occurrence in collections is governed to a large extent by chance. In contrast, Kendall's W compared abundance rankings of the major taxa, and indicated an underlying pattern of uniformity.

It must also be remembered, that these tests, like any statistical procedures, are only as good as the data on which they are based. In the present study, the data available were derived from intensive, systematic sampling over a period of 18 months (24 months in the case of Noone Creek), but even so the chance collection of rare species in particular can be expected to have influenced the statistics. Nevertheless, I believe that the non-parametric procedures used were appropriate, as the observations were not necessarily independent, or drawn from normally distributed populations with equal variances. Also, non-parametric tests are often more conservative than equivalent parametric tests and one is more likely to accept the null hypothesis, when it is in fact false (ie. a Type II error; Siegel 1956).

E. Temporal variation in benthic invertebrate assemblages

Overall, benthic assemblages at all sites differed qualitatively through time (as indicated by Cochran's Q values in Table 6.9c). This apparent lack of temporal persistence in faunal composition at three sites could either be a seasonal phenomenon, the result of chance collection or non-collection of rare taxa, or the result of more immediate environmental factors affecting the distribution and/or density patterns of taxa, especially rare ones.

**Table 6.9.** Comparisions of temporal variability in composition (presence/absence data) of the 4 stream faunas using Cochran's Q test for a) Surber samples only, b) cobble samples only and c) all benthic samples (Surber, cobble and kick samples). $H_0$: probability of taxon being recorded was similar over time and ** indicates that $p < 0.01$ and $H_0$ rejected, ie. faunal composition differed among dates.

| | | Noone | Mapourika | Jetty | Steep |
|---|---|---|---|---|---|
| a) Taxa in Surber samples only | Q | 37.8 | 27.9 | 50.9 | 15.1 |
| | df | 13 | 10 | 10 | 9 |
| | p | < 0.01 | < 0.01 | < 0.01 | > 0.05 |
| | $H_0$: | reject** | reject** | reject** | accept |
| b) Taxa in cobble samples only | Q | 34.4 | 13.7 | 8.0 | 8.8 |
| | df | 11 | 8 | 6 | 6 |
| | p | < 0.01 | > 0.05 | > 0.05 | > 0.05 |
| | $H_0$: | reject** | accept | accept | accept |
| c) Taxa in all benthic samples | Q | 49.4 | 71.5 | 57.2 | 3.0 |
| | df | 13 | 10 | 10 | 9 |
| | p | < 0.01 | < 0.01 | < 0.01 | < 0.01 |
| | $H_0$: | reject** | reject** | reject** | reject** |

The first possibility, the influence of seasonal factors can be disregarded, as few taxa occured at only restricted times of year.

However, the chance collection or non-collection of "rare" taxa included in the comparative analysis may have had an influence on the Q statistic. For example, 81 taxa were recorded from Noone Creek during the study, but only 15 taxa had relative abundances greater than 1 percent of all invertebrates collected in Surber samples (Table 6.3), and the number of taxa collected on any one occasion ranged from 22 to 40.

**Table 6.10.** Quantitative comparisons of temporal variability in faunal composition as indicated by Kendall's W, based on major taxa (relative abundance greater than 1%) in a) Surber samples with, b) without *Deleatidium* and Chironomidae; and c) in cobble samples. $H_0$: abundance rankings of major taxa differed among dates and ** indicates that $p < 0.01$ and $H_0$ was rejected. NC - W could not be calculated if there were less than two major taxa.

| | Noone Ck. W,df | Mapourika Ck. W,df | Jetty Ck. W,df | Steep Ck. W,df |
|---|---|---|---|---|
| a) | 0.45, 14 ** | 0.49, 12 ** | 0.80, 8 ** | 0.67, 14 ** |
| b) | 0.23, 12 ** | 0.14, 10 ns | 0.47, 6 ** | 0.60, 12 ** |
| c) | 0.45, 6 ** | 0.61, 4 ** | NC | 0.79, 4 ** |

Kendall's coefficients of concordance (W) calculated from the abundance rankings of major taxa on all sampling occasions are shown in Table 6.10. At all sites, the invertebrate assemblages could be regarded as persistent through time as indicated by the significant values of Kendall's W. When *Deleatidium* and Chironomidae were excluded, indices were generally lower but still statistically significant, although at Mapourika Creek, there was no longer significant agreement in faunal rankings through time. The persistence of *Deleatidium* and Chironomidae as the most abundant taxa at almost all times is a particularly notable feature of all four stream assemblages.

F. Life history patterns of selected benthic insects

Head capsule width (HCW) was used as an index of body size of nine insect taxa whose size-frequency distributions were examined from November 1984 to May 1986 (November 1984 - November 1986 at Noone Creek). Ephemeroptera, Plecoptera and Trichoptera collected in all benthic samples (1 kick, 5 cobble and 5 Surber samples per sampling date per site) were used for the analysis. Because small individuals were probably collected less effectively than larger ones with the 0.25 mm mesh net employed, their relative proportions in the populations are likely to be underestimates.

Final instars of ephemeropteran and plecopteran taxa were identified by the development of their wingpads, but earlier instars of these taxa could not be determined from HCW measurements. Temporal changes in size-frequency distributions of these taxa are presented graphically using linear HCW measurements (ie. mm) plotted on a logarithmic y-axis. The latter presentation technique was used by Cowie (1980) to clarify patterns of nymphal growth of some New Zealand Plecoptera, and acknowledges that growth proceeds in a geometric fashion because of the normally constant factor of increase at each moult (ecdysis quotient).

Head capsule measurements were not usually satisfactory for discriminating larval instars of caddisflies taken in field collections. Therefore, most size groupings used were based on limited instar measurement data provided by Michaelis (1974).

(i) *Deleatidium* spp.

Seasonal size-frequency distributions of *Deleatidium* nymphs collected in benthic samples from the four sites are shown in Figure 6.8. Total numbers of nymphs collected on each sampling occasion varied among the sites (Fig. 6.2-6.5), and ranged from 15 to 402. Several indistinguishable species of *Deleatidium* may be included in this taxon, but the majority of nymphs taken at each site were morphologically consistent and belonged to the informal "*lillii* group" of Winterbourn & Gregson (1981).

Nymphal instars could not be determined on the basis of HCW, but final instars could be distinguished on the basis of wingpad length. Individuals about to emerge had blackened wingpads and were collected in very small numbers at all sites (Noone Creek - 2 nymphs, Mapourika Creek - 4, Jetty Creek - 1, Steep Creek - 2). Final instar nymphs spanned a considerable size range (HCW 1.44-2.08 mm), and the maximum size of nymphs at Noone and Jetty Creeks (HCW 1.76-1.92 mm) was less than at the other streams (HCW 1.92-2.08 mm).

At all sites, a wide size range of nymphs was present on all dates and bimodal size distributions were often recorded. They indicated periods when large numbers of small nymphs had been recruited into the population before larger nymphs of the previous cohort had emerged. Recruitment of small nymphs occurred throughout the year, but peaked during autumn and winter, when the highest densities were also found. Large nymphs (and those with black wingpads) occurred in benthic samples from August to May, but some recently emerged *Deleatidium* adults were collected and/or observed throughout the year. No peak in abundance of adults was observed.

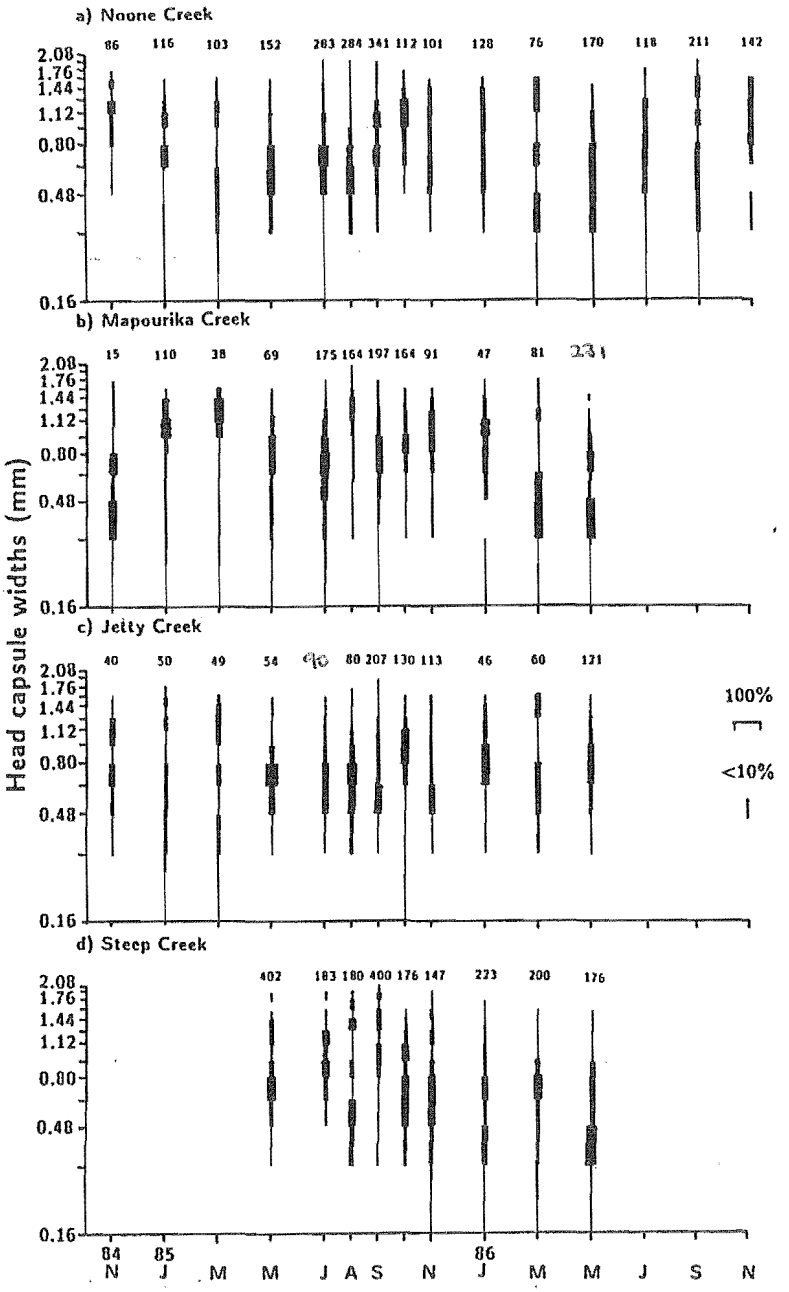



Figure 6.8. Changes in size frequency distributions of *Deleatidium* nymphs collected in benthic samples between November 1984 and November 1986 from a) Noone, b) Mapourika, c) Jetty and d) Steep Creeks. Labelling for all X-axes indicated on d). Distributions plotted on a logarithmic y-axis. Numerals above histograms show samples sizes.

Growth patterns of *Deleatidium* cohorts were difficult to interpret from the size-frequency data obtained at the four sites. Data from Noone Creek suggested that two overlapping and poorly defined annual generations (one summer and one winter cohort) may have been present, with the summer cohort (November to March) having much faster growth than the winter one (March to November/January). A summer generation at Mapourika Creek was more easily distinguished in 1984-85 but recruitment in autumn 1985 was not as strong as in autumn 1986. Size-frequency distributions from Jetty and Steep Creeks were more obscure and showed no indications of cohort growth or emergence and small nymphs were present at most times of year.

(ii) *Coloburiscus humeralis*

The life history was investigated only at Noone Creek, where numbers of nymphs collected on each date ranged from 5 to 123. As for *Deleatidium*, instars could not be distinguished on the basis of head capsule width.

The size-frequency data presented in Figure 6.9, indicate that the life cycle of *C. humeralis* was univoltine and the same general pattern of population growth was apparent in the 1985 and 1986 generations. Nevertheless, a wide range of different sized nymphs was present in most months despite the low numbers of animals collected on many days. The main period of emergence and recruitment of new individuals suggested by the data is January - May.

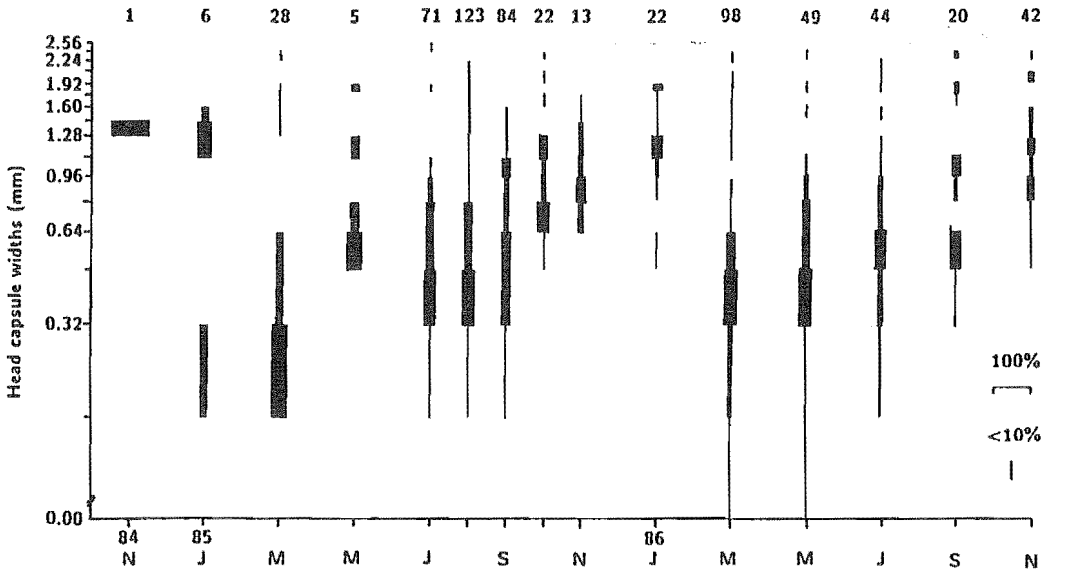



Figure 6.9. Changes in size frequency distributions of *Coloburiscus humeralis* nymphs collected in benthic samples between November 1984 and November 1986 from Noone Creek. Numerals show sample sizes.

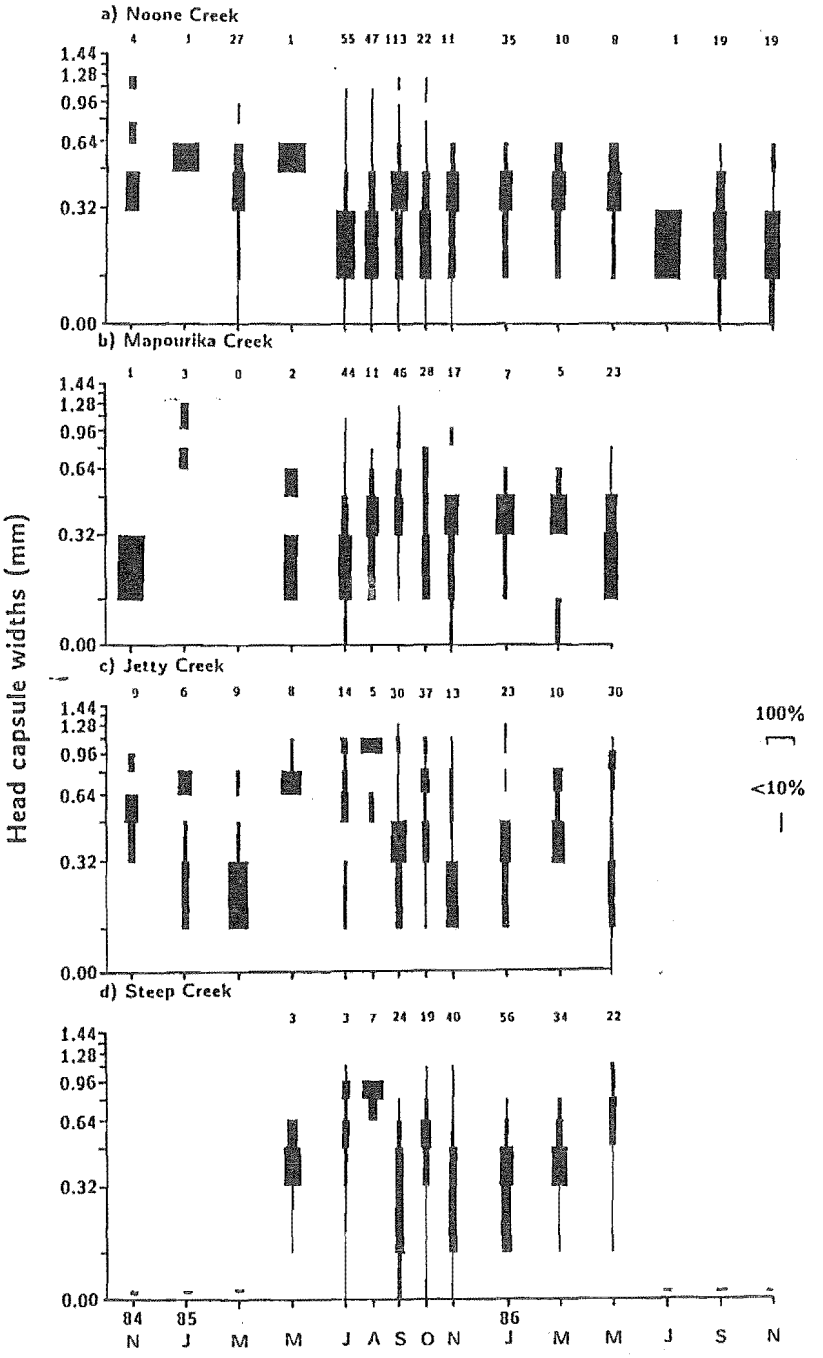



Figure 6.10. Changes in size frequency distributions of *Zelandobius confusus* nymphs collected in benthic samples between November 1984 and November 1986 from a) Noone, b) Mapourika, c) Jetty and d) Steep Creeks. Labelling for all X-axes indicated on d). Numerals above histograms show sample sizes.

(iii) *Zelandobius confusus*

Size-frequency distributions of *Z. confusus* populations at the four sites are presented in Figure 6.10. Few nymphs were present at most sites and interpretation of the size frequency distributions was difficult. Size distributional data suggest a univoltine life history for *Z. confusus* populations at all sites with cohorts overlapping during summer.

At Noone and Mapourika Creeks, small nymphs dominated in most months and emergence appeared to occur during late winter and spring (August -November). Although higher proportions of large individuals were present at Jetty Creek, small nymphs were found throughout the year as at the other two sites. At Steep Creek, growth of a major cohort was apparent from summer through autumn 1986, and data from the previous year suggest that emergence would have occurred in late winter.

In Devils Creek, North Westland, Cowie (1980) found distinct cohorts of *Z. confusus* with a clearly univoltine life cycle. Rapid growth of nymphs occurred during autumn and early winter and final instars were most common over winter, as in my South Westland streams. Adults were collected from August to October and early instar larvae shortly thereafter. Cowie's findings were similar to those reported by Winterbourn (1978) for a *Z. confusus* population in Middle Bush stream, Cass, except that he found adults in September only.

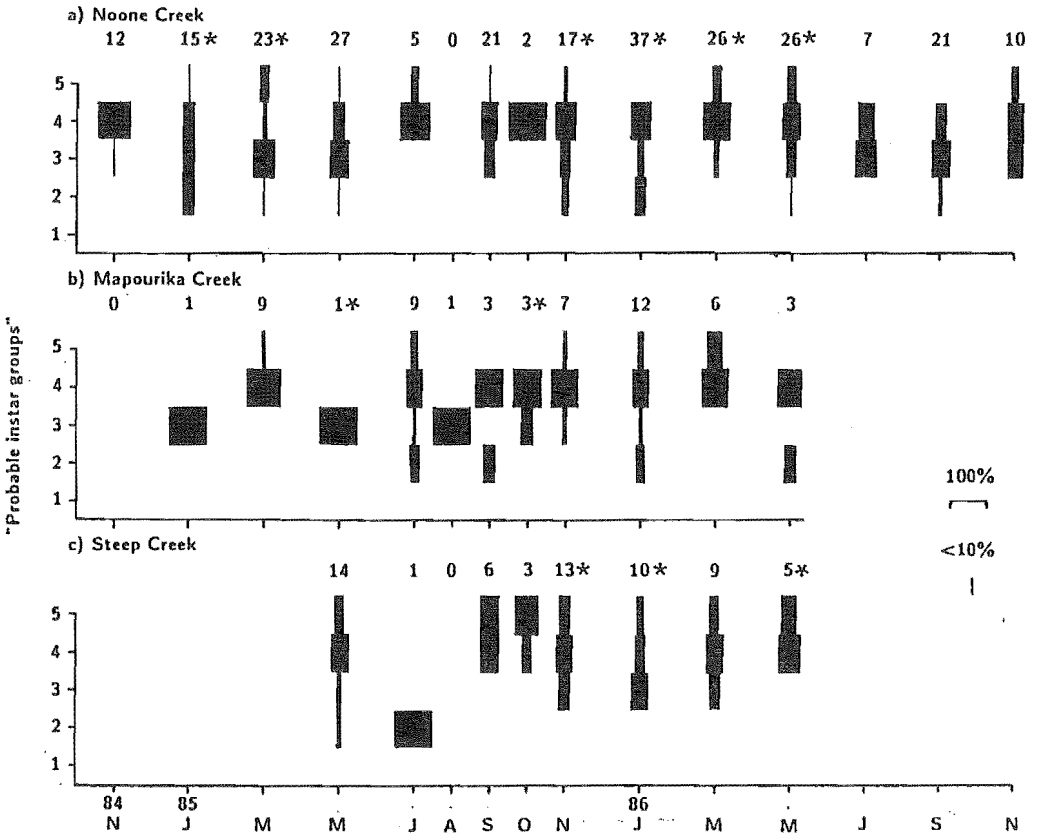



Figure 6.11. Changes in "probable instar group" distributions of *Rakiura vernale* collected in benthic samples between November 1984 and November 1986 from a) Noone, b) Mapourika and c) Steep Creeks. Labelling for all X-axes indicated on c). Numerals above histograms show samples sizes, - no samples collected and * pupae collected.

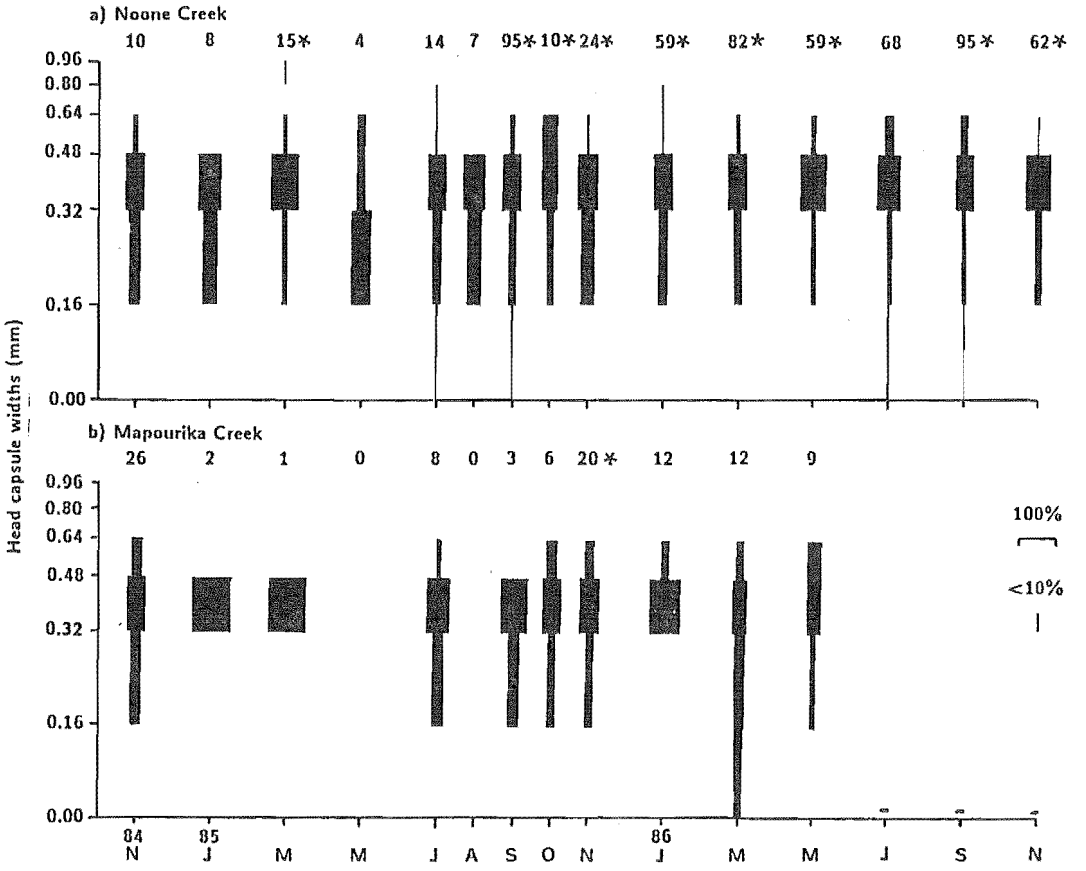



Figure 6.12. Changes in size frequency distributions of *Helicopsyche poutini* collected in benthic samples between November 1984 and November 1986 from a) Noone and b) Mapourika Creeks. Labelling for all X-axes indicated on b). Distributions plotted on a logarithmic y-axis. Numerals above histograms show samples sizes, - no samples collected and * pupae collected.

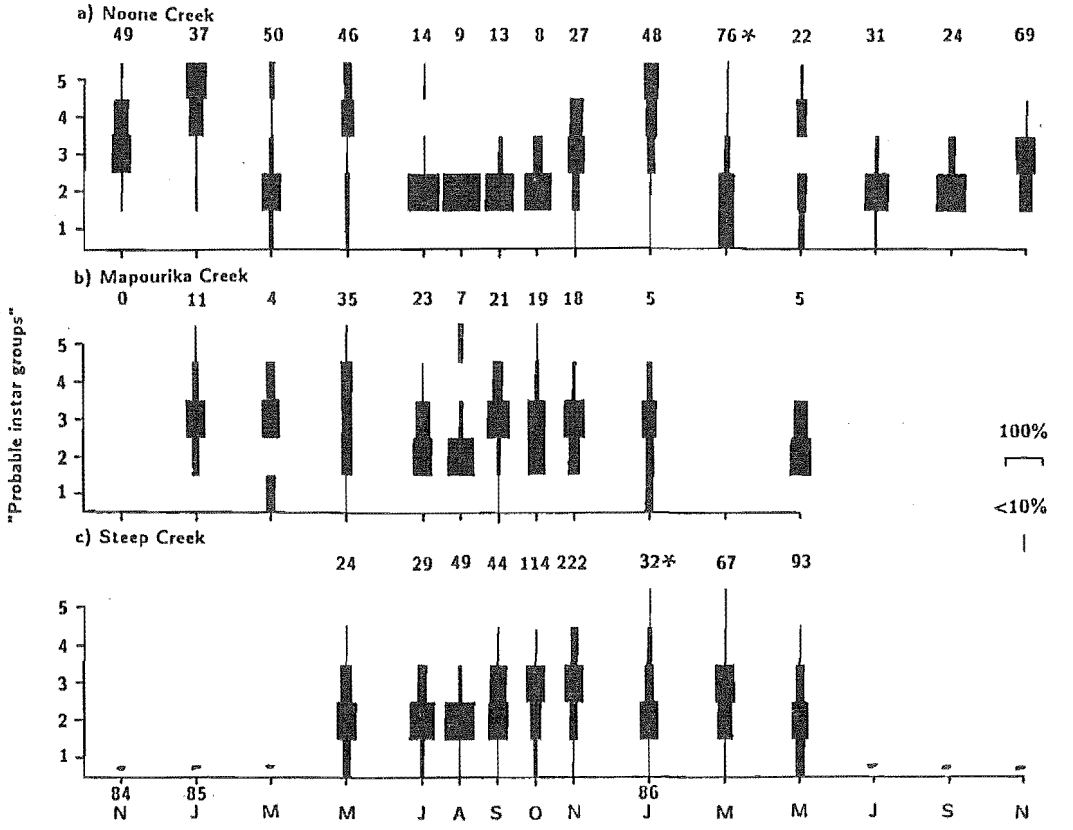



Figure 6.13. Changes in "probable instar group" distributions of *Zelolessica cheira* collected in benthic samples between November 1984 and November 1986 from a) Noone, b) Mapourika and c) Steep Creeks. Labelling for all X-axes indicated on c). Numerals above histograms show sample sizes, - no samples collected and * pupae collected.

(iv) *Rakiura vernale*

Larvae of *R. vernale* were found in low to moderate densities (up to 37 per site per date) in all streams except Jetty Creek. Head capsule width measurements did not discriminate instars and the probable instars suggested by Michaelis (1973) are used in portraying size distribution data (Table 6.11).

The life history pattern of *R. vernale* was clearest at Noone Creek where most larvae were taken (Fig. 6.11). Numbers of large larvae and pupae peaked in March 1985 and 1986, and in May 1986. Small larvae were apparently recruited during late winter and spring, grew slowly during summer and pupated the following autumn. In Mapourika and Steep Creeks, a wide size range of larvae was present on most occasions and periods of recruitment and emergence were impossible to determine from the size distributions.

Table 6.11. Mean head capsule widths (HCW) and quotient of ecdysis for larval instars of *R. vernale* reported by Michaelis (1973), and the "probable instar groups" used in Figure 6.11.

| "Instar" | Mean HCW (mm) (Michaelis 1973) | Probable instar groups (mm) (Figure 6.11) |
|---|---|---|
| Final | 1.04 | 0.81-1.12 |
| F-1 | ? | 0.49-0.80 |
| F-2 | ? | 0.33-0.48 |
| F-3 | 0.25 | 0.17-0.32 |
| F-4 | 0.15 | ? |
| Quotient of ecdysis | | 1.67 |

Michaelis (1973) found that in Waikoropupu Springs *R. vernale* overwintered as pupae. Adult emergence occurred in early spring and the flight period lasted for less than four weeks. Eggs and hatchlings

were collected shortly after this time and larval growth occurred mainly in summer and autumn.

(v) *Helicopsyche poutini*

*H. poutini* was not found at Jetty and Steep Creeks but size-frequency distributions are shown for Noone and Mapourika Creeks (Fig. 6.12). Instars could not be separated using HCW measurements and size distributions were therefore plotted as linear HCW measurements on a logarithmic y-axis.

At both streams, larvae of various sizes were present in most months. However, at Noone Creek, recruitment of small larvae occurred mainly during late winter and spring, although large larvae and pupae were found throughout the year. At Mapourika Creek, the smallest larvae were taken in March (autumn), although no major cohort could be identified. This suggests that *H. poutini* exhibited some temporal variability in recruitment between the two sites.

(vi) *Zelolessica cheira*

*Z. cheira* was present at all sites, but was most common at Noone and Steep Creeks. Mean head capsule widths for instars reported by Michaelis (1974, Table 6.12) were used as a basis for allocating larvae to "probable instar groups".

A univoltine life history with slow winter and spring growth was indicated by collections of larvae from Noone and Steep Creeks. At Noone Creek, large larvae were most common in summer and autumn (Fig. 6.13a) and in both 1985 and 1986 instar distributions were bimodal in autumn when new larval recruits and larvae from the previous year class were present together. First instar larvae were also most common in

Steep Creek in May of both years. At Mapourika Creek, where a wide size range of larvae including small individuals was present in most months.

Table 6.12. Mean head capsule widths (HCW) and quotient of ecdysis for larval instars of *Z. cheira* reported by Michaelis (1974), and the "probable instar groups" used in Figure 6.13.

| Instar | Mean HCW (mm) (Michaelis 1974) | Probable instar groups (mm) (Figure 6.13) |
|---|---|---|
| Final | 0.70 | 0.65 - 0.96 |
| F-1 | 0.45 | 0.49 - 0.64 |
| F-2 | 0.25 | 0.33 - 0.48 |
| F-3 | 0.15 | 0.0 - 0.32 |
| F-4 | ? | ? |
| Quotient of ecdysis | | 1.5 - 1.57 |

The life history of *Z.cheira* was more clearly defined in Waikoropupu Springs (Michaelis 1974). Second instar larvae were found mainly in early winter, instars III and IV became more abundant during winter and spring and abundance of final instar larvae peaked in spring and summer. This is fairly similar to the pattern observed in South Westland, although final instar larvae may persist further into autumn in this more southerly location.

G. Annual production of benthic invertebrates

The term production, as used here, refers to the total biomass of organic matter transformed and added to the community during any given period. Larval production was calculated by the size-frequency method (Benke 1984) and a modified version of the instantaneous growth method (Hopkins 1976). Because growth patterns and generation times of

invertebrate cohorts were difficult or impossible to identify, other potentially more accurate methods of calculating production could not be used.

The size-frequency method (SFM) was designed to estimate production of species or species groups in which cohorts could not be readily identified, and involved summing the losses in biomass from one size class to the next for all classes. The method assumes that all individuals in the species group of interest are of equivalent voltinism, and to obtain annual production estimates corrections must be made if species have other than 1-year cycles. Furthermore, the method assumes that all individuals must be capable of growing to the same maximum size and that growth of individuals (measured by size increases) is linear. This final assumption is unlikely to hold for insects but Hamilton (1969) demonstrated that non-linear growth does not seriously affect production estimates.

In contrast to the SFM, the Hopkins' method (HM) is a modification of the instantaneous growth method used by Ricker (1946) and Allen (1951) to calculate fish production. Hopkins' method estimates invertebrate production for a given time period which must include at least one generation of the taxon. Both growth and mortality are assumed to be exponential and inversely related during this time. Annual production (P) is calculated by multiplying mean annual biomass (B) by instantaneous growth rate (G) of the population calculated as the natural logarithm of the ratio of mean maximum and minimum weights of individuals recorded during the sampling period (P=GB). The method was used by Hopkins (1976) to assess annual production of nine invertebrate taxa in two New Zealand streams, and resulted in estimates ranging from 0.54 to 20.68 $g.m^{-2}.y^{-1}$. These values compared favourably with those calculated from the same

data with the size frequency method (0.69-20.83 $g.m^{-2}.y^{-1}$).

Annual production, standing crops and turnover ratios of six aquatic insect taxa were calculated where possible for two or three overlapping, 12-month periods; January 1985 - January 1986 (Year 1), May 1985 - May 1986 (Year 2) and November 1985 - November 1986 (Year 3 - Noone Creek only). By using three non-calender "years" limited temporal comparisons within populations were possible. Mean maximum and minimum size data used in the calculations of production for the six taxa are shown in Table 6.13. All taxa whose annual production was calculated were assumed to have one generation per year, although clearly this was difficult to substantiate (see life history interpretations above).

**Table 6.13.** Mean minimum and maximum dry weights (mg) of 6 taxa used to calculate their instantaneous growth rates.

| | Noone | Mapourika | Jetty | Steep |
|---|---|---|---|---|
| *Deleatidium* | 0.01,1.55 | 0.01,1.79 | 0.01,1.79 | 0.01,1.55 |
| *C. humeralis* | 0.01,3.11 | | | |
| *Z. confusus* | 0.09,0.76 | 0.09,0.87 | 0.09,0.87 | 0.09,0.76 |
| *R. vernale* | 0.07,0.28 | 0.07,0.28 | | 0.07,0.24 |
| *H. poutini* | 0.07,0.24 | 0.07,0.21 | | |
| *Z. cheira* | 0.08,2.11 | 0.08,1.68 | 0.08,1.68 | 0.08,1.68 |

(i) *Deleatidium* spp.

Estimates of annual production, standing crop (or biomass) and turnover ratio are given for each stream in Table 6.14. Calculated annual production rates (size frequency method) and standing crops ranged from 1.95 to 3.67 g $DW.m^{-2}.y^{-1}$ and 0.50 to 0.95 g $DW.m^{-2}$, respectively, and were highest at Noone Creek and lowest at Jetty Creek. With the Hopkins' method, production estimates ranged from 2.21 to 4.06 $gDW.m^{-2}.y^{-1}$, and

except at Steep Creek were always slightly higher than those calculated with the size frequency method.

Table 6.14. Estimates of production, annual biomass, instantaneous growth rate and turnover ratio for *Deleatidium* populations in the four streams.

| | Noone | Mapourika | Jetty | Steep |
|---|---|---|---|---|
| **Production ($g.m^{-2}.y^{-1}$)** | | | | |
| a) Size frequency method | | | | |
| Jan 1985 - Jan 1986 | 3.32 | 3.04 | 1.95 | |
| May 1985 - May 1986 | 3.67 | 3.28 | 2.26 | 3.58 |
| Nov 1985 - Nov 1986 | 2.81 | | | |
| b) Hopkins' method | | | | |
| Jan 1985 - Jan 1986 | 4.06 | 3.15 | 2.21 | |
| May 1985 - May 1986 | 3.88 | 3.29 | 2.57 | 3.46 |
| Nov 1985 - Nov 1986 | 3.39 | | | |
| **Annual biomass ($g.m^{-2}$)** | | | | |
| Jan 1985 - Jan 1986 | 0.95 | 0.70 | 0.50 | |
| May 1985 - May 1986 | 0.91 | 0.73 | 0.59 | 0.79 |
| Nov 1985 - Nov 1986 | 0.77 | | | |
| **Instantaneous growth rate** | | | | |
| Jan 1985 - Jan 1986 | 4.249 | 4.494 | 4.376 | |
| May 1985 - May 1986 | 4.249 | 4.494 | 4.376 | 4.494 |
| Nov 1985 - Nov 1986 | 4.376 | | | |
| **Turnover ratio (P/B)** | | | | |
| a) Size frequency method | | | | |
| Jan 1985 - Jan 1986 | 3.49 | 4.34 | 3.90 | |
| May 1985 - May 1986 | 4.03 | 4.49 | 3.86 | 4.53 |
| Nov 1985 - Nov 1986 | 3.65 | | | |
| b) Hopkins' method | | | | |
| Jan 1985 - Jan 1986 | 4.25 | 4.49 | 4.38 | |
| May 1985 - May 1986 | 4.25 | 4.49 | 4.38 | 4.49 |
| Nov 1985 - Nov 1986 | 4.38 | | | |

At all sites, *Deleatidium* production estimates were higher in "year 2" (May 1985-May 1986), when *Deleatidium* densities were also higher, than in "year 1" (January 1985-January 1986). However, annual production and standing crop of the *Deleatidium* population at Noone Creek was lowest in

"year 3" (November 1985-November 1986), despite the attainment of higher average densities in that period (Fig. 6.2b).

Head capsule widths of final instar nymphs with black wingpads, were larger at Mapourika and Steep Creeks (1.92-2.08 mm) than at Noone and Jetty Creeks (1.76-1.92 mm) and the higher instantaneous growth rates at Mapourika and Steep Creeks reflect this difference (Table 6.14). Turnover ratios were marginally higher at Mapourika and Steep Creeks than Noone and Jetty Creeks, although at all sites they were in the range 3.48 to 4.52.

(ii) *Coloburiscus humeralis*

This filter-feeding mayfly was only found at Noone Creek. Calculated estimates of annual production, standing crop and turnover ratios for the Noone Creek population ranged from 1.44 to 2.16 (SFM), 1.36 to 1.90 $gDW.m^{-2}.y^{-1}$ (HM), 0.24 to 0.34 $gDW.m^{-2}$ and 6.00 to 6.97 (SFM) and 5.68 to 5.76 (HM), respectively (Table 6.15).

Annual production rates, standing crops and turnover ratios were higher in "years 2 and 3" than "year 1" although densities were similar among "years" (x= 27.$m^{-2}$, 34.$m^{-2}$, 37.$m^{-2}$).

Although the standing crop and calculated rates of annual production for *C. humeralis* populations were less than half those of *Deleatidium* at Noone Creek, both turnover ratios and instantaneous growth rates were higher. The lower annual production and biomass reflect the lower densities of *C. humeralis* at Noone Creek, but the higher instantaneous growth rates and turnover ratios may, at least in part, be a consequence of the larger body size of this mayfly compared to *Deleatidium*. Although densities were low, life history data suggested that a cohort of

*C.humeralis* takes about 12 months to grow from hatchling to final instar nymph (Fig. 6.9).

**Table 6.15.** Estimates of production, annual biomass, instantaneous growth rate and turnover ratio for *C.humeralis* in Noone Creek.

| | Noone |
|---|---|
| Production ($g.m^{-2}.yr^{-1}$) | |
| a) Size frequency method | |
| Jan 1985 - Jan 1986 | 1.44 |
| May 1985 - May 1986 | 2.16 |
| Nov 1985 - Nov 1986 | 2.13 |
| b) Hopkins' method | |
| Jan 1985 - Jan 1986 | 1.36 |
| May 1985 - May 1986 | 1.78 |
| Nov 1985 - Nov 1986 | 1.95 |
| Annual biomass ($g.m^{-2}$) | |
| Jan 1985 - Jan 1986 | 0.24 |
| May 1985 - May 1986 | 0.31 |
| Nov 1985 - Nov 1986 | 0.34 |
| Instantaneous growth rate | |
| Jan 1985 - Jan 1986 | 5.760 |
| May 1985 - May 1986 | 5.760 |
| Nov 1985 - Nov 1986 | 5.682 |
| Turnover ratio (P/B) | |
| a) Size frequency method | |
| Jan 1985 - Jan 1986 | 6.00 |
| May 1985 - May 1986 | 6.97 |
| Nov 1985 - Nov 1986 | 6.26 |
| b) Hopkins' method | |
| Jan 1985 - Jan 1986 | 5.76 |
| May 1985 - May 1986 | 5.76 |
| Nov 1985 - Nov 1986 | 5.68 |

(iii) *Zelandobius confusus*

Annual production and standing crop of *Z. confusus* populations were an order of magnitude lower than for *Deleatidium* at all sites (Table 6.16), although turnover ratios were similar. Both standing crops and production of *Z. confusus* populations were highest at Noone and Jetty

Creeks and lowest at Mapourika Creek, and they were higher in "year 2" than "year 1" at all sites. Production and standing crop was much lower at Noone Creek in "year 3" than "years 1 and 2", even though mean population density was higher.

Table 6.16. Estimates of production, annual biomass, instantaneous growth rate and turnover ratio for *Z. confusus* in the four streams.

| | Noone | Mapourika | Jetty | Steep |
|---|---|---|---|---|
| **Production ($g.m^{-2}.y^{-1}$)** | | | | |
| a) Size frequency method | | | | |
| Jan 1985 - Jan 1986 | 0.35 | 0.15 | 0.34 | |
| May 1985 - May 1986 | 0.45 | 0.19 | 0.38 | 0.29 |
| Nov 1985 - Nov 1986 | 0.10 | | | |
| b) Hopkins' method | | | | |
| Jan 1985 - Jan 1986 | 0.22 | 0.11 | 0.09 | |
| May 1985 - May 1986 | 0.28 | 0.14 | 0.17 | 0.21 |
| Nov 1985 - Nov 1986 | 0.07 | | | |
| **Annual biomass ($g.m^{-2}$)** | | | | |
| Jan 1985 - Jan 1986 | 0.11 | 0.05 | 0.09 | |
| May 1985 - May 1986 | 0.14 | 0.07 | 0.12 | 0.10 |
| Nov 1985 - Nov 1986 | 0.04 | | | |
| **Instantaneous growth rate** | | | | |
| Jan 1985 - Jan 1986 | 2.050 | 2.185 | 1.427 | |
| May 1985 - May 1986 | 2.050 | 2.185 | 1.427 | 2.050 |
| Nov 1985 - Nov 1986 | 1.707 | | | |
| **Turnover ratio (P/B)** | | | | |
| a) Size frequency method | | | | |
| Jan 1985 - Jan 1986 | 3.31 | 3.00 | 3.94 | |
| May 1985 - May 1986 | 3.30 | 2.84 | 3.27 | 2.78 |
| Nov 1985 - Nov 1986 | 2.29 | | | |
| b) Hopkins' method | | | | |
| Jan 1985 - Jan 1986 | 2.05 | 2.18 | 1.43 | |
| May 1985 - May 1986 | 2.05 | 2.18 | 1.43 | 2.05 |
| Nov 1985 - Nov 1986 | 1.71 | | | |

Differences in the instantaneous growth rates calculated for this species at the four sites reflect the different sizes attained in the

respective streams. Estimates of annual production obtained with the Hopkins' method (0.07-0.28 $gDW.m^{-2}.y^{-1}$) were always smaller than those calculated with the size-frequency method (0.10-0.45 $gDW.m^{-2}.y^{-1}$) and were most discrepant at Jetty Creek where maximum nymphal size, and consequently the instantaneous growth factor, was smallest.

(iv) *Rakiura vernale*

Throughout the study, the helicopsychid, *R. vernale* occurred in low densities at Noone, Mapourika and Steep Creeks (0-62 $m^{-2}$) and both annual production calculated by the SFM and biomass were low (less than 0.05 $gDW.m^{-2}.y^{-1}$ and 0.02 $gDW.m^{-2}$, respectively; Table 6.17). Production was slightly higher in Noone Creek than at the other sites.

(v) *Helicopsyche poutini*

Production estimates were calculated for the Noone and Mapourika Creek populations only, as larvae were not found at the other sites. *H. poutini* was more productive than *R. vernale* at Noone and Mapourika Creeks, and calculated turnover ratios (3-4) were also twice those calculated for the *R. vernale* populations (Table 6.18). Larvae attained a larger size at Noone Creek than Mapourika Creek and this difference was reflected by the larger instantaneous growth rate values calculated for the former site.

In both streams, the lower production in "Year" 1 was associated with lower densities of larvae and the presence of fewer larger individuals, ie. lower mean population biomass.

Table 6.17. Estimates of production, annual biomass, instantaneous growth rate and turnover ratio for *R. vernale* in three streams.

| | Noone | Mapourika | Steep |
|---|---|---|---|
| **Production ($g.m^{-2}.y^{-1}$)** | | | |
| a) Size frequency method | | | |
| Jan 1985 - Jan 1986 | 0.03 | 0.02 | |
| May 1985 - May 1986 | 0.04 | 0.01 | 0.02 |
| Nov 1985 - Nov 1986 | 0.04 | | |
| b) Hopkins' method | | | |
| Jan 1985 - Jan 1986 | 0.02 | 0.01 | |
| May 1985 - May 1986 | 0.03 | 0.01 | 0.01 |
| Nov 1985 - Nov 1986 | 0.02 | | |
| **Annual biomass ($g.m^{-2}$)** | | | |
| Jan 1985 - Jan 1986 | 0.02 | 0.01 | |
| May 1985 - May 1986 | 0.02 | 0.01 | 0.01 |
| Nov 1985 - Nov 1986 | 0.02 | | |
| **Instantaneous growth rate** | | | |
| Jan 1985 - Jan 1986 | 1.203 | 1.334 | |
| May 1985 - May 1986 | 1.334 | 1.334 | 1.203 |
| Nov 1985 - Nov 1986 | 1.334 | | |
| **Turnover ratio (P/B)** | | | |
| a) Size frequency method | | | |
| Jan 1985 - Jan 1986 | 1.50 | 2.00 | |
| May 1985 - May 1986 | 2.00 | 1.00 | 2.00 |
| Nov 1985 - Nov 1986 | 2.00 | | |
| b) Hopkins' method | | | |
| Jan 1985 - Jan 1986 | 1.20 | 1.33 | |
| May 1985 - May 1986 | 1.33 | 1.33 | 1.20 |
| Nov 1985 - Nov 1986 | 1.33 | | |

Table 6.18. Estimates of production, annual biomass, instantaneous growth rate and turnover ratio for *H.poutini* in two streams.

| | Noone | Mapourika |
|---|---|---|
| **Production ($g.m^{-2}.y^{-1}$)** | | |
| a) Size frequency method | | |
| Jan 1985 - Jan 1986 | 0.10 | 0.02 |
| May 1985 - May 1986 | 0.15 | 0.04 |
| Nov 1985 - Nov 1986 | 0.13 | |
| b) Hopkins' method | | |
| Jan 1985 - Jan 1986 | 0.04 | 0.01 |
| May 1985 - May 1986 | 0.05 | 0.01 |
| Nov 1985 - Nov 1986 | 0.04 | |
| Annual biomass ($g.m^{-2}$) | | |
| Jan 1985 - Jan 1986 | 0.04 | 0.01 |
| May 1985 - May 1986 | 0.04 | 0.01 |
| Nov 1985 - Nov 1986 | 0.04 | |
| Instantaneous growth rate | | |
| Jan 1985 - Jan 1986 | 1.203 | 1.052 |
| May 1985 - May 1986 | 1.203 | 1.052 |
| Nov 1985 - Nov 1986 | 1.203 | |
| Turnover ratio (P/B) | | |
| a) Size frequency method | | |
| Jan 1985 - Jan 1986 | 2.50 | 2.00 |
| May 1985 - May 1986 | 3.75 | 4.00 |
| Nov 1985 - Nov 1986 | 3.25 | |
| b) Hopkins' method | | |
| Jan 1985 - Jan 1986 | 1.20 | 1.05 |
| May 1985 - May 1986 | 1.20 | 1.05 |
| Nov 1985 - Nov 1986 | 1.20 | |

(vi) *Zelolessica cheira*

Estimates of annual production, standing crop and turnover ratios for *Z.cheira* are given for all four streams in Table 6.19. Steep and Noone Creek populations were at least four times more productive (0.69-1.25 $gDW.m^{-2}.y^{-1}$) than those at Mapourika and Jetty Creeks (0.15-0.17

gDW.$m^{-2}.y^{-1}$). Turnover ratios at all four sites were between 3 and 4 and no differences in production were apparent among "years".

Table 6.19. Estimates of production, annual biomass, instantaneous growth rate and turnover ratio for *Z.cheira* in four streams

| | Noone | Mapourika | Jetty | Steep |
|---|---|---|---|---|
| Production ($g.m^{-2}.yr^{-1}$) | | | | |
| a) Size frequency method | | | | |
| Jan 1985 - Jan 1986 | 0.92 | 0.16 | 0.12 | |
| May 1985 - May 1986 | 0.69 | 0.17 | 0.15 | 1.25 |
| Nov 1985 - Nov 1986 | 0.71 | | | |
| b) Hopkins' method | | | | |
| Jan 1985 - Jan 1986 | 0.98 | 0.13 | 0.06 | |
| May 1985 - May 1986 | 0.67 | 0.14 | 0.08 | 0.91 |
| Nov 1985 - Nov 1986 | 0.63 | | | |
| Annual biomass ($g.m^{-2}$) | | | | |
| Jan 1985 - Jan 1986 | 0.31 | 0.04 | 0.04 | |
| May 1985 - May 1986 | 0.21 | 0.05 | 0.05 | 0.30 |
| Nov 1985 - Nov 1986 | 0.20 | | | |
| Instantaneous growth rate | | | | |
| Jan 1985 - Jan 1986 | 3.214 | 2.981 | 1.552 | |
| May 1985 - May 1986 | 3.214 | 2.981 | 1.552 | 2.981 |
| Nov 1985 - Nov 1986 | 3.214 | | | |
| Turnover ratio (P/B) | | | | |
| a) Size frequency method | | | | |
| Jan 1985 - Jan 1986 | 2.97 | 4.00 | 3.00 | |
| May 1985 - May 1986 | 3.29 | 3.40 | 3.00 | 4.16 |
| Nov 1985 - Nov 1986 | 3.55 | | | |
| b) Hopkins' method | | | | |
| Jan 1985 - Jan 1986 | 3.21 | 2.98 | 1.55 | |
| May 1985 - May 1986 | 3.21 | 2.98 | 1.55 | 2.98 |
| Nov 1985 - Nov 1986 | 3.21 | | | |

(vii) Summary

Annual production, standing crop biomass and population densities of most taxa were greatest at Noone and Steep Creeks and lowest at Mapourika and Jetty Creeks.

Densities and production were also higher in "year 2" (May 1985 - May 1986) than "year 1" (January 1985 - January 1986) for all taxa except *Z. cheira* for which production was highest in "year 1" at Noone Creek. The level of production in "year" 3 (Noone Creek only, November 1985 - November 1986) varied depending on the taxon concerned; values for *Deleatidium*, *Z. confusus* and *Z. cheira* were lowest in "year 3", whereas estimates obtained for *C. humeralis*, *R. vernale* and *H. poutini* were lower than in "year 2" but not "year 1". Differences in production among the "years" may reflect differences in environmental conditions experienced during the study period (eg. flooding, drought) and differences in the strengths of year classes. However, differences were small and could simply be due to sampling error rather than be a real phenomenon.

For most taxa, production values obtained with the Hopkins' method were slightly lower than those obtained with the size-frequency method; the only exception was *Deleatidium*. Hopkins (1976) also observed this difference when he calculated production for nine invertebrate taxa (including *Deleatidium*, *C. humeralis* and *H. poutini*) with the two techniques (SFM and HM). Hopkins (1976) believed that the lower estimates obtained with his method were the result of inadequate sampling of small individuals and an inability to determine the voltinism of invertebrate taxa accurately. A premise of the Hopkins' method is that mortality rates decrease exponentially as the invertebrates grow, however, it is unclear how accurate an assumption this is for stream invertebrate populations in the flood-prone South Westland region of the

South Island. Choice of the maximum-size-attained value to be used in calculations is also critical as it determines G (the instantaneous growth rate factor) and the magnitude of the largest size group delineated in the SFM. I used the average weight of individuals in the maximum size group in an attempt to minimize errors introduced in this way. Despite the limitations of the different methods and the data sets available, the production estimates obtained with these methods were very similar and suggest that the Hopkins' technique, which requires less detailed sample analysis, is a viable alternative to the SFM in situations where the latter has become the method of choice.

Chapter Seven

# SYNTHESIS and DISCUSSION

Hynes (1975) stated that "every stream is likely to be an individual" as a result of the topography, vegetation, climate and geology of its catchment. Accordingly, these four factors were taken into consideration when I was selecting the present study streams. Those chosen in the Lake Mapourika - Okarito River catchment have similar geology, climate (including rainfall) and catchment vegetation, but catchment size, catchment and stream channel slope, size of bed materials and degree of riparian shading differed among them.

All four streams drained small, headwater catchments (100-200 ha) at an altitude of 100 m above sea level, but they possessed contrasting flow conditions. Streamflow was more turbulent in the streams with steep catchments and predominantly cobble and boulder beds (Mapourika, Jetty and Steep) than in Noone Creek which had a lower gradient and a bed dominated by finer sediments.

The streams all had slightly acid water (pH range 4.5 - 6.5), little carbonate buffering capacity, and moderate to high concentrations of dissolved organic carbon (DOC) which gave the water a distinctly brown appearance. Chemical "signatures" (*sensu* Collier 1988b) differed slightly among streams. Alkalinity, pH and conductivity were highest at Mapourika Creek and lowest at Jetty and Steep Creeks. DOC concentration was usually greatest at Noone and Steep Creeks and lowest at Mapourika Creek. Amounts of organic material retained within the streambeds were low, ranging from 3 to 58 gAFDW.$m^{-2}$ on different dates, and no

relationship with site, season or flow conditions prior to sampling was apparent.

Biomass of epilithic assemblages was also low in all four streams and was typically composed of a mixture of diatoms, filamentous algae, bacteria, and amorphous organic particles. Total epilithic biomass was similar among the four streams (*ca.* 60-110 $ugC.cm^{-2}$), but the proportion of biologically active material, as indicated by oxygen change measurements, differed among the streams and was highest at Noone Creek.

Changes in physico-chemical conditions and epilithic biomass showed no seasonal patterns, but were correlated with flow conditions at the time of, or prior to sampling. Epilithic biomass was not correlated with pH, DOC, POC or any other measured water chemistry parameters and the absence of such associations also point to flow and associated factors (ie. substratum movement) being of major importance. On a small scale, this was demonstrated experimentally using 3-tiered tile holders on which substrates were incubated under three inundation regimes in Noone and Jetty Creeks. SEM examination of epilithic assemblages that developed under the three submergence regimes showed that they were qualitatively similar in each stream and at each height, but that algal biomass was up to nine times higher on continuously submerged tiles than on those that were rarely submerged.

Grazing by invertebrates may also have at least a minor influence on epilithic biomass in these streams as indicated by grazer-exclusion trials carried out in Noone Creek, the stream with the least variable flow and highest densities of invertebrate grazers (mean annual density $42.m^{-2}$). In three 2-month long experiments, results clearly indicated that invertebrate grazers reduced epilithic biomass as TOC levels on

"ungrazed" substrata were on average twice those on surfaces exposed to "normal grazing pressures".

Taxon richness and densities of benthic invertebrates recorded in the four streams were moderately low (86 taxa, 400-1200 invertebrates $m^{-2}$). Taxon richness was always highest at Noone Creek, and lowest at Jetty (50) and Steep Creeks (50), whereas benthic densities were higher at Noone and Steep Creeks than at Mapourika and Jetty Creeks. No seasonal patterns in benthic densities were evident. Two composite taxa, Chironomidae and *Deleatidium* dominated the faunas of all four streams, and comprised between 58 and 77 percent of the invertebrates collected in Surber samples. Another 22 taxa were considered to be "major" taxa, that is, they each comprised more than 1 percent of the invertebrates in the Surber samples at a particular stream. The remaining 62 taxa were defined as "rare".

Faunal composition (numbers and kinds of taxa) differed qualitatively among the streams, and among sampling periods (although this was probably, in part, a consequence of inefficient collection of rare taxa). However, relative abundances of the 24 major taxa (including the two dominants) were similar among all streams. These abundance rankings did not change significantly over the course of the study.

In summary, it is apparent that in terms of their general water chemistry, and epilithic and faunal assemblages, the four streams had much in common. However, Noone Creek, differed from the others with respect to size of bed materials, epilithic algal diversity, and richness of benthic invertebrate fauna, and it appears that the greater constancy, or continuity of flow experienced at this site is the key to its distinctiveness.

A. Comparisons with other New Zealand stream studies

The ecology of benthic invertebrates and the nature of assemblages in various types of New Zealand streams and rivers were reviewed recently by Winterbourn (1986) in "Inland Waters in New Zealand". He noted that "because of its regular and abundant rainfall and extensively dissected mountainous terrain, New Zealand is endowed with an abundance of rivers and streams." The size and steepness of the country means that most river systems are short and swift-flowing with gravel and boulder strewn beds, and many New Zealand streams experience marked fluctuations in flow. This is especially true on the western slopes of the Southern Alps, where rainfall is particularly high (1700-7000 mm per annum).

Physical stability of the stream environment was considered by Towns (1976), Cowie (1980) and Rounick (1982) to be of prime importance in structuring stream invertebrate assemblages. In fact, both Towns (1976) and Cowie (1980) observed that diverse assemblages tended to be associated with relatively stable physical environments. Rounick & Winterbourn (1983) assessed the relationship between faunal composition and the physical stability of stream environments using the Pfankuch stream reach stability procedure (Pfankuch 1975) and found that in streams with stability index values of greater than 100 (that is, with poor to fair stability of physical conditions (Pfankuch 1975)), invertebrate shredders were absent, possibly because the capacity of the streams to retain coarse particulate organic material (CPOM) and provide suitable habitat for shredders, was inadequate. Collier & Winterbourn (1987) subsequently found that the streambed component of the Pfankuch stability index was negatively associated with the extent of temporal variability of invertebrate densities of four flood-prone West Coast

streams, a finding that provides further support for the contention that physical stability is a primary assemblage structuring determinant. I also found that invertebrate taxon richness was negatively correlated with streambed and lower banks scores of the Pfankuch stability index (see Appendix One for further details).

My four study streams scored between 73 and 93 on the Pfankuch scale and would be described as good to fair on his 4-state descriptive scale (poor, fair, good and excellent). Steep Creek had the highest score, and Jetty Creek the lowest, indicating they were the least and most stable streams, respectively. The stream channel stability rankings did not correspond well with observed flow continuity patterns, however, and as indicated earlier in this discussion, flow continuity ( or relative constancy of flow) appears to be a key factor influencing epilithic and invertebrate assemblage size and structure. Thus, although the Pfankuch procedure does provide a comparative evaluation of stream channel stability, it provides only a coarse index of instream conditions with respect to benthic flora and fauna.

As a consequence of their marked physical instability, the benthic faunas of many New Zealand streams are dominated by invertebrate species which feed primarily as fine particle collectors and/or by browsing stone surface organic layers (Winterbourn *et al.* 1981, Winterbourn 1982). Consequently, the diversity or richness of stream faunas could partially depend on the quality and quantity of the epilithon. Epilithic assemblages in acidic streams elsewhere have been considered to be impoverished in terms of biomass and algal diversity (Patrick *et al.* 1968), however, in South Westland, such characteristics may be more the result of variable flow conditions than water chemistry. In the Lake Mapourika-Okarito River streams, epilithic biomass was reduced during

periods of high rainfall, presumably due to the tumbling of substrata and abrasion of fine sediments during high flows, as described by Scrimgeour & Winterbourn (in press) in the much larger Ashley River. It is also possible that algal populations are nitrogen limited, at least to a limited extent, as indicated by nutrient diffusion experiments carried out in Noone, Jetty and Steep Creeks by Winterbourn *et al.* (1988) and Winterbourn (unpublished data).

Collier & Winterbourn (1987) found that epilithic algal biomass (estimated from chlorophyll and phaeophytin measurements) was generally greater in clearwater than brownwater streams in the part of South Westland where I worked. Their results confirmed that algal populations were composed predominantly of a few acid-tolerant diatom species and filamentous algae (eg. *Tribonema, Oedogonium*). Collier & Winterbourn (1987) suggested that the apparently lower quality epilithon of brownwater streams may influence the absolute and relative abundances of benthic macro-invertebrates and my finding of relatively sparse benthic assemblages in brownwater streams agree with this suggestion.

The abundant rainfall and frequent flooding that is characteristic of South Westland also results in poor retention of organic material (BOM) within the streambeds as was evident in all four study streams (annual means between 15 and 26 gAFDW.$m^{-2}$). BOM values obtained for other New Zealand streams are listed in Table 7.1 and range from 27 to 496 gAFDW.$m^{-2}$. Estimates from two small mountain streams (Rounick & Winterbourn 1982) and two Southland streams draining hill country tussock grasslands (Ryder 1983) were considerably higher than those from my study sites but collections of BOM were made from them on only two occasions. On the other hand, BOM standing biomass in the South Westland streams was similar to that found in the braided Ashley River on the Canterbury

Plains (Scrimgeour 1987) where BOM was collected every month for a year. The available evidence indicates that retention in New Zealand streams is low on a world-wide basis (Bott *et al.* 1985), because of their variable and harsh flow conditions.

Table 7.1. Summary of the results of New Zealand studies in which benthic organic material (BOM) stored within the streambed was measured. Values have been converted to comparable dry weight units, where necessary.

| Stream (Reference) | BOM ($gAFDW.m^{-2}$) | Comments |
|---|---|---|
| Middle Bush Stream (Rounick & Winterbourn 1982) | 496, 108 | 15 Surber samples; collected in April and July 1982. |
| Craigieburn Cutting Stream (Rounick & Winterbourn 1982) | 108, 27 | 15 Surber samples; collected in April and July 1982. |
| Two Southland hill country streams draining tussock grasslands (Ryder 1983) | 105, 233* | 3 core samples; collected in February and March 1983. |
| Ashley River (Scrimgeour 1987) | 30 | 5 Surber samples; collected monthly from May 1985 to April 1986. |
| Four brownwater streams in South Westland | 15-26 | 5 Surber samples; collected every 2 months from January 1985 to November 1986. |

* originally expressed as $gC.m^{-2}$.

The benthic faunal assemblages in my flood-prone, brownwater streams have moderately low taxon richness and densities, as was reported by Collier & Winterbourn (1987) and Winterbourn & Collier (1987) for other West Coast streams. Taxonomic richness was particularly low compared with the Waitakere River (Towns 1979) and Devils Creek systems (Cowie

1985), where 144 and 138 invertebrate taxa were identified, respectively. However, taxon richness of the brownwater streams was similar to that found in the intensively sampled, braided Rakaia (Sagar 1983, 1986; 33 taxa) and Ashley Rivers (Scrimgeour 1987; 57 taxa), and the forested, sub-alpine Middle Bush Stream, Cass, where 45 taxa were identified (Winterbourn 1978, 1982).

The recent work by Winterbourn & Collier (1987) on the distribution of stream invertebrates in forested Westland streams indicated that they might be influenced more by the regional location of the site than measured physico-chemical conditions of the streams (pH, conductivity, alkalinity, DOC). Thus, the very similar faunas in my study streams may be strongly influenced by their close proximity to each other (less than 20 km apart), and therefore the probable availability of a common pool of colonists.

Life history data obtained for selected benthic invertebrate taxa in the four study streams indicated a propensity for poorly defined population growth and either non-seasonal or weakly synchronized life cycles. This is consistent with the findings of Towns (1981, 1983b), Cowie (1980), Winterbourn (1978, 1982) and Collier (1988a) for numerous taxa in a variety of New Zealand streams. Cowie (1980) found that five out of six stonefly species he studied had poorly synchronized seasonal cycles and long flight periods in the physically-unstable and flood-prone Devils Creek, North Westland. Further south, Collier (1988) found that a wide size range of *Deleatidium* larvae were present throughout the year in four streams with variable flows. The non-seasonal and weakly synchronized life histories of New Zealand stream invertebrates have been attributed to the oceanic and unpredictable nature of New Zealand's climate, the general lack of pulsed leaffall and the poor retention

capacity of the streams (Towns 1981, 1983b, Winterbourn 1986), and ensures that individuals in many life history stages are available to recolonize streams at almost any time of year.

Finally, much research in stream ecology over the last decade has emphasised biological productivity and attempted to quantify functional relationships and energy flows between trophic levels (Waters 1977, 1979, Benke 1984). Several New Zealand studies (Hopkins 1976, Scrimgeour 1987, Collier 1988) have reported annual production values for invertebrate taxa that were common in my study streams (Table 7.2). Secondary production values I calculated for *Deleatidium* spp. ranged from 1-3 $gAFDW.m^{-2}.y^{-1}$, and were similar to those reported by Hopkins (1976) for four of his five sites and Collier (1988) for three of his South Westland sites. However, Scrimgeour (1987) reported estimates of *Deleatidium* production an order of magnitude higher in the braided Ashley River, where two annual cohorts were identified. Production estimates for a *Deleatidium* population on the wave beaten shores of sub-alpine Lake Grasmere (Grieg 1976) were nearly twice those from South Westland and values for another Canterbury river population (Winterbourn 1974) were three times higher again (Table 7.2). Estimates of secondary production for another mayfly, *C.humeralis* common to both Hopkins' and my studies, were three to four times greater in the North Island streams than in Noone Creek, where only a small population was present.

Biological factors such as high diversity, unavailability of life history information, and practical limitations of sampling programs, have impeded detailed studies of secondary production on whole stream assemblages. Few workers have attempted to estimate total macro-invertebrate production in a section of stream (Nelson & Scott 1962, Hopkins 1976, Neves 1979, Krueger & Waters 1983, Benke *et al.* 1983,

Behmer & Hawkins 1986, Williams & Hogg 1988), but those values that have been reported range from 5 to 74 gAFDW. $m^{-2}.y^{-1}$. Estimates I have made for the four South Westland streams (≈10 gAFDW.$m^{-2}.y^{-1}$) are at the low end of this range.

Table 7.2. Production estimates for *Deleatidium* spp., *Coloburiscus humeralis*, and entire benthic faunas in New Zealand.

| Taxon | Stream(s) (Reference) | Production estimates (gAFDW.$m^{-2}.y^{-1}$) |
|---|---|---|
| *Deleatidium* | Hinau Str.<br>Horokiwi Str.<br>(Hopkins 1976) | 7.7 (open site), 1.8, 6.5 (forested site)<br>2.5 (open site), 2.5 (forested site) |
| | Lake Grasmere<br>(Greig 1976) | 5.9 |
| | Selwyn River<br>(Winterbourn 1974) | 19.6* |
| | Ashley River<br>(Scrimgeour 1987) | 44.5 |
| | 4 streams in South Westland (Collier 1988) | 2.5, 3.7, 3.8, 10.4 |
| | 4 brownwater streams in South Westland (present study) | 3.3, 3.2, 2.1, 3.6 |
| *C. humeralis* | North Branch of Hinau Stream<br>(Hopkins 1976) | 7.1 (9.6) |
| | Noone Creek, South Westland (present study) | 1.9 (1.7) |
| Total fauna | Horokiwi Stream<br>(Allen 1951) | 228-612 g wet wt.$m^{-2}.y^{-1}$** |
| | Hinau Str.<br>Horokiwi Str.<br>(Hopkins 1976) | 74 (open site), 8, 33 (forested sites)<br>44, 57 (open sites), 25 (forested site) |
| | 4 brownwater streams in South Westland (present study) | 10# |

* recalculated by Collier (1988).
** calculated from biomass and turnover ratio data in Allen (1951).
# estimate based on sum of production values of major taxa.

In the only New Zealand study in which a serious attempt was made to estimate total bottom fauna production, Hopkins (1976) obtained values of 8-32 $gAFDW.m^{-2}.y^{-1}$ for forested, headwater reaches, and 44-74 $gAFDW.m^{-2}.y^{-1}$ for open, downstream reaches of the Hinau and Horokiwi streams in the southern North Island. In an earlier study, Allen (1951) found that "average stock" of bottom fauna in a single reach of the Horokiwi Stream ranged between 0.4 and 1.1 g wet $wt.m^{-2}$. Using his data on invertebrate consumption by trout, Allen suggested that the annual turnover ratio ($P/\hat{B}$) of the benthic fauna must be at least 100, however, Gerking (1962) later showed that this value was an overestimate by a factor of two or three. Even then, benthos production in the Horokiwi would be much higher than calculated there by Hopkins (1976) 30 years later.

B. Environmental stability and assemblage structure

In stream systems, environmental stability is often viewed as the propensity for the physical environment to be disturbed or altered. Disturbance is difficult to define and measure at the level of the ecosystem, and stream ecologists have had particular difficulty with this concept. The degree of variability of environmental conditions (in particular rainfall and streamflow) provides a measure of the stability of the stream environment.

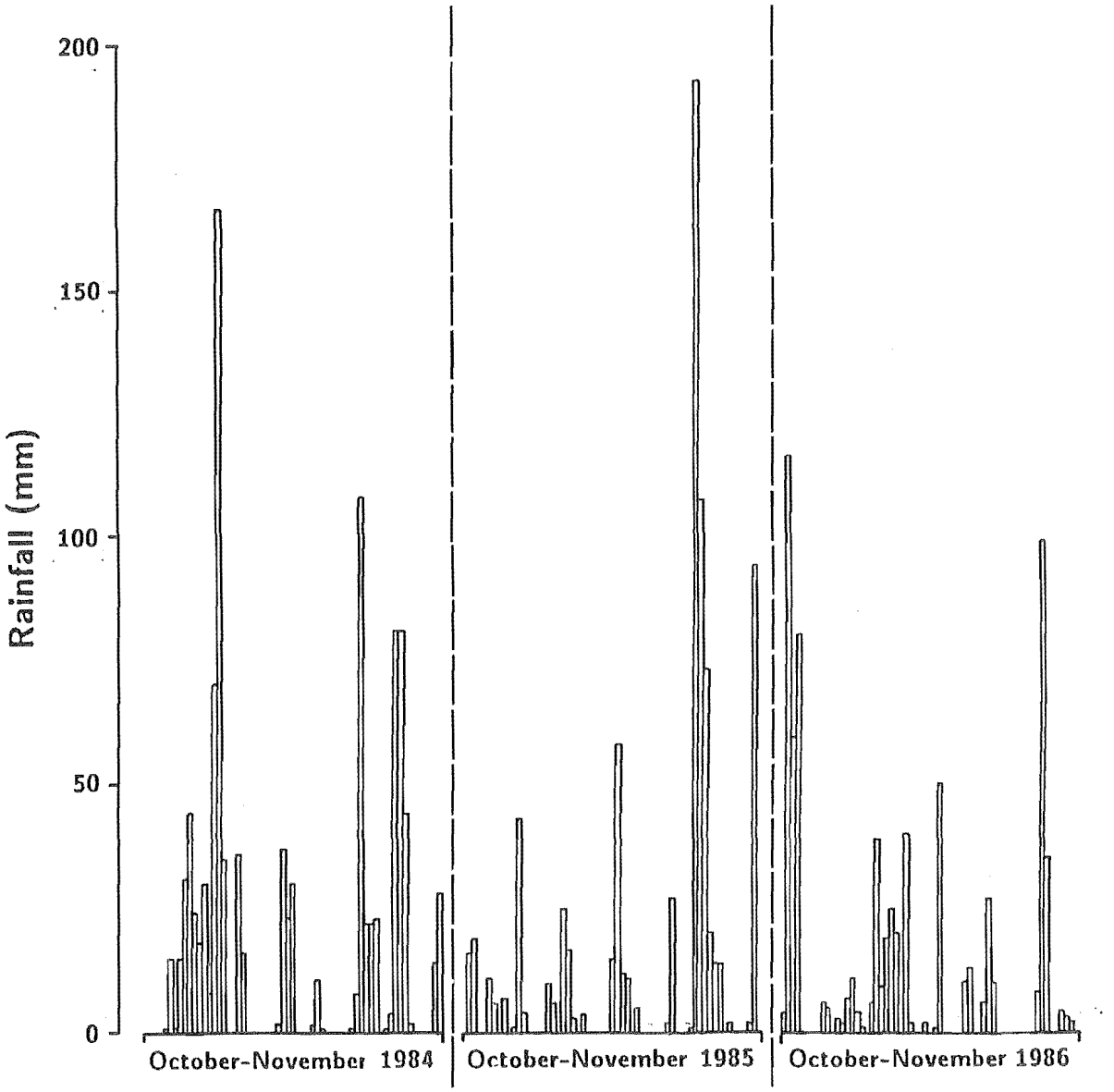



Figure 7.1. Daily rainfall in two months (October & November) for three consecutive years (1984, 1985 & 1986) recorded at the township of Franz Josef Glacier (ca 20 km south of the study area).

Like many streams in South Westland, the four study streams were subject to frequent and unpredictable fluctuations in flow (annual rainfall 5236 mm; 177 annual raindays), which in turn affected the water chemistry of the streams. Analysis of eleven years (January 1976 -December 1986) of monthly rainfall data collected at the Franz Josef Glacier township (20 km south of the study area) showed that monthly rainfall was high throughout the year, although rainfall fluctuates markedly from day to day (Figure 7.1).

Streamflow, the other measure of environmental stability, was related to rainfall as expected, and both stream discharge and percentage wetted streambed were measured to compare flow continuity among the four streams. The term "flow continuity" is used to denote persistence of flow within a defined channel. During the study period (November 1984 -November 1986), absolute streamflows were highest at Mapourika Creek, whereas continuity of flow was most marked at Noone Creek, which also tended to be the least "flashy" of the four streams.

Two measures were used to describe macro-invertebrate assemblage stability: a) persistence, a measure of the presence or absence of taxa over time and b) constancy of relative abundances of species over time (ie. stability of taxon rankings). They were assessed using two non-parametric tests of association; Cochran's Q and Kendall's coefficient of concordance (W).

Low persistence of assemblage composition was found during the study period (ie. over 18 or 24 months) in all streams ($Q > 27$, $df = 10$ ) except Steep Creek ($Q = 15$, $df = 9$). However, the relative abundances of the major taxa remained constant ($W > 0.45$) even though absolute population sizes fluctuated. The results highlight several notable features of the stream faunas. First, a small group of major taxa was abundant in all

four streams and taxa defined as rare formed a large proportion (72%) of the total. The large numbers of rare taxa (whose collectability owed more to chance) influenced the persistence measure more than the small group of abundant taxa, as found by other stream biologists in New Zealand (eg. Winterbourn 1978, Cowie 1980) and elsewhere (eg. Meffe & Minckley 1986, Townsend & Hildrew 1988), and emphasises the importance of assessing temporal constancy of assemblage structure in terms of the abundance rankings of major taxa and not merely presence/absence of all taxa.

The question of temporal stability of assemblage structure has been examined for various subsets of animals in a number of different ecosystems including streams (Grossman *et al.* 1982, Meffe & Minckley 1986, Townsend *et al.* 1987, Hughes 1987), the marine intertidal zone (Grossman 1982, Sousa 1984), and North American grasslands (Joern & Pruess 1986). The stream studies noted above were carried out in environmental conditions ranging from unpredictable to seasonal, and are commented upon below.

Meffe & Minckley (1986) examined assemblage stability of fish and invertebrate populations in an unregulated Sonoran Desert stream, Aravaipa Creek which was subjected to frequent and intense flooding, mainly during summer. Even though absolute population sizes fluctuated, stability of taxon rankings (measured by Kendall's W) was high in both assemblages. From their study it appeared that life history and behavioural attributes of the fauna compensated for seasonally occurring disturbances, and this is probably true too of the invertebrate fauna in the flood-prone South Westland streams.

Temporal persistence of stream faunas was assessed by Townsend *et al.* (1987) at 27 stream sites in southern England by comparing surveys

carried out eight years apart. They found that species composition and relative abundances of major species had changed markedly between surveys, however, faunal persistence was greatest at low discharge, upstream sites with cool summer temperature regimes and low, stable pH. Their findings suggest that persistence of faunal assemblages should be low in streams with highly variable flow regimes, but this was not the case (during an 18 or 24 month period) in my flood-prone South Westland streams.

Hughes (1987) monitored changes in aquatic macrophyte assemblages for 28 months in two east coast Tasmanian streams with unpredictable hydrological regimes. In this region, annual rainfall is low (<1500 mm per annum), and although few storms occur those that do are intense and can be at any time of year. Hughes found that both stability and persistence of macrophyte assemblages were low during the period studied, and were a consequence of the unpredictable hydrological regime.

As in the study of Meffe & Minckley (1986), more than one generation of stream invertebrates would have grown and developed to maturity during the period of my study, and two rainfall events severe enough to be classified by the local weather office as "100 year floods" occurred. Assemblage characteristics of the four streams were therefore documented at a time when the potential for destruction was very high, yet in contrast to Hughes' macrophtye "communities", South Westland invertebrate assemblages were shown to be temporally persistent and resilient to flood events. In terms of the terminology of Lake & Barmuta (1986) they were clearly "determinate" assemblages, whose component populations displayed a high degree of resistance to physical disturbance or resilience following perturbation.

## ACKNOWLEDGEMENTS

Financial assistance for this research was provided by the Department of Conservation, Forest Service (Westland Conservancy) and Zoology Department, University of Canterbury and I am grateful for their generous assistance.

Numerous people have helped me during this study and their assistance is much appreciated. First of all, I extend my sincere thanks to my supervisor, Dr Mike Winterbourn, whose guidance, humour and patience I have sorely taxed, especially during the past 12 months. His accessability and interest in my thesis encouraged me through many rough patches and the final manuscript owes much to his constructive criticisms.

I thank the Stream Team and others (A. Frutiger, C. Lively, M. Wells), who provided convivial field assistance. Discussions with Mike, members of the Stream Team, and other members of the Zoology Department (both students and staff) have helped to develop and clarify ideas presented in this thesis. Several people volunteered to read parts of the draft manuscript: Kevin Collier, Russell Death, Paul Rainey, Allen Rodrigo and Mark Wells; and I thank them for their useful comments. Much appreciated statistical advice was provided by Drs McLay and Duncan, Allen Rodrigo and Mark Wells.

The expertise and friendly advice of the technical staff in the Zoology Department was also greatly appreciated. In particular, my thanks go to Bruce and his predecessor Jack (the stores people), Jan (the SEM expert), Joan (advisor on thesis presentation and production), Lyn and Tracey (patient teachers of Volkswriter 3), and Sandy and Dave (constructors of various sampling devices).

I thank Dr. Eric Spurr of the Forest Research Institute, Ilam for the use of field facilities at Okarito and Westland National Park Information Centre, Franz Josef Glacier for rainfall records at Franz Josef Glacier during my study. Drs Biggs, Broady, Johns and Winterbourn are thanked for the identifications of algal and insect material. Roger Waite is thanked for the generous loan of his computer.

During the writing of my thesis, I know that I placed considerable strain on my friends and family and I thank them all for their good-natured tolerance. In particular, I thank Alastair for hogging the rain, Ilse and Rainer for always being willing to distract me, Jan, Chris and Roger for their patience with a "crotchety" flatmate, Lynda for the healthy competition, Margaret for encouraging me to swim and Tracey for Sunday night TV dinners. Extra-special thanks go to Paul Rainey for making me eat regularly at Varsity (and his support and good humour) over the last year.

# REFERENCES

ALLEN, K.R. (1951) The Horokiwi stream: a study of a trout population. *New Zealand Marine Department, Fisheries Bulletin* 10.

BEHMER, D.J. & C.P. HAWKINS. (1986) Effects of overhead canopy on macro-invertebrate production in a Utah stream. *Freshwater Biology* 16: 287-300.

BENKE, A.C. (1984) Secondary production of aquatic insects. p. 289-322. *In* The Ecology of Aquatic Insects. Ed. by Resh, V.H. & D.M. Rosenberg. Praeger, New York, U.S.A.

BENKE, A.C., T.C. VAN ARSDALL, & D.M. GILLESPIE. (1984) Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* 54: 25-63.

BISHOP, J.E. (1973) Limnology of a small Malayan River Sungai Gombak. W.Junk, The Hague.

BOTT, T.L., J.T. BROCK, C.S. DUNN, R.J. NAIMAN, R.W. OVINK, & R.C. PETERSEN. (1985) Benthic community metabolism in four temperate stream systems: An interbiome comparison and evaluation of the river continuum concept. *Hydrobiologia* 123: 3-45.

CASWELL, H.L. (1976) Community structure: a neutral model analysis. *Ecological Monographs* 46: 327-354.

CLEMENTS, F.C. (1916) Plant succession: an analysis of the development of vegetation. Carnegie Institute of Washington, Publication No. 242. Stanford, California, U.S.A.

CODY, M.L. (1974) Competition and the Structure of Bird Communities. Princeton University Press, Princeton, New Jersey, U.S.A.

COLLIER, K.J. (1987a) Spectral properties of some West Coast waters and their relationship with dissolved organic carbon. *Mauri Ora* 14: 25-32.

COLLIER, K.J. (1987b) Spectrophotometric determination of dissolved organic carbon in some South Island streams and rivers. *New Zealand Journal of Marine and Freshwater Research* 21:349-351.

COLLIER, K.J. (1988a) Ecology of acid brownwater streams in Westland, New Zealand. Unpublished Ph.D. thesis, University of Canterbury, Christchurch, New Zealand.

COLLIER, K.J. (1988b) Stone surface organic layers in naturally acid and alkaline streams in South Westland, New Zealand. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie* 23.

COLLIER K.J. & M.J. WINTERBOURN. (1987) Faunal and chemical dynamics of some acid and alkaline New Zealand streams. *Freshwater Biology* 18: 227-240.

COLWELL, R.K. (1985) The evolution of ecology. *American Zoologist* 25: 771-777.

CONNELL, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

CONNELL, J.H. & E. ORIAS. (1964) The ecological regulation of species diversity. *American Naturalist* 98: 399-414.

CONNELL, J.H. & W.P. SOUSA. (1983) On the evidence needed to judge ecological stability or persistence. *American Naturalist* 121: 789-824.

COOPER, S.D. & T.L. DUDLEY. (1988) The interpretation of "controlled" vs "natural" experiments in streams. *Oikos* 52: 357-361.

COWIE, B. (1980) Community dynamics of the benthic fauna in a West Coast stream ecosystem. Unpublished Ph.D. thesis, University of Canterbury, Christchurch, New Zealand.

COWIE, B. (1985) An analysis of changes in the invertebrate community along a southern New Zealand montane stream. *Hydrobiologia* 120: 35-46.

COWLEY, D.R. (1978) Studies on the larvae of New Zealand Trichoptera. *New Zealand Journal of Zoology* 5: 639-750.

CUMMINS, K.W. (1974) Structure and function of stream ecosystems. *BioScience* 24: 631-641.

CUMMINS, K.W. & G.H. LAUFF. (1969) The influence of substrate particle size on the micro-distribution of stream macro-benthos. *Hydrobiologia* 34: 145-181.

DAYTON, P.K. (1971) Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351-389.

DOEG, T. & P.S. LAKE. (1981) A technique for determining the composition and density of macro-invertebrate fauna of large stones in streams. *Hydrobiologia* 80: 3-6.

DUDLEY, T.L., S.D. COOPER, & N. HEMPHILL. (1986). Effects of macroalgae on a stream invertebrate community. *Journal of the North American Benthological Society* 5: 93-106.

ELLIOTT, J.M. (1971) Distances travelled by drifting invertebrates. *Oecologia* 6: 350-379.

ELTON, C.S. (1958) The Ecology of Invasion by Plants and Animals. Chapman & Hall, London, U.K.

FISHER, S.G. (1983) Succession in streams. p. 7-28. *In* Stream Ecology: Application and Testing of General Ecological Theory. Ed. by Barnes, J.R. & G.W. Minshall. Plenum, New York, U.S.A.

FISHER, S.G. & L.J. GRAY. (1983) Secondary production and organic matter processing by collector macro-invertebrates in a desert stream. *Ecology* 64: 1217-1224.

FISHER, S.G., L.J. GRAY, N.B. GRIMM, & D.E. BUSCH. (1982) Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52: 93-110.

FISHER, S.G. & N.B. GRIMM. (1988) Disturbance as a determinant of structure in a Sonoran desert stream ecosystem. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie* 23.

GARDNER, M.R. & W.R. ASHBY. (1970) Connectance of large, dynamic (cybernetic) systems: critical values for stability. *Nature* 228: 784.

GERKING, S.D. (1962) Production and food utilization in a population of bluegill sunfish. *Ecological Monographs* 32: 31-78.

GLEASON, H.A. (1926) The individualistic concept of plant association. *Bulletin of the Torrey Botanical Club* 53: 7-26.

GOLTERMAN, H.L. (1970) Methods for Chemical Analysis of Fresh Waters. IBP handbook No. 8. Blackwell Scientific Publications, Oxford, U.K.

GRASSLE, J.F. & H.L. SANDERS. (1973) Life history and the role of disturbance. *Deep Sea Research* 20: 643-659.

GRAY, L.J. (1981) Species composition and life history of aquatic insects in a lowland Sonoran desert stream. *American Midland Naturalist* 106: 229-242.

GRAY, L.J. & S.G. FISHER. (1981) Post flood recolonization pathways of macro-invertebrates in a lowland Sonoran desert stream. *American Midland Naturalist* 106: 249-257.

GRAY, L.J. & J.V. WARD. (1982) Effects of sediment releases from a reservoir on stream macro-invertebrates. *Hydrobiologia* 96: 177-184.

GREIG C.A. (1976) Ecology of *Deleatidium* sp. (Ephemeroptera) in Lake Grasmere, Canterbury, with particular reference to its trophic relationships. Unpublished M.Sc. thesis, University of Canterbury, Christchurch, New Zealand.

GREIG-SMITH, P. (1983) Quantitative Plant Ecology. 3rd edition. Blackwell Scientific Publishers, Oxford, U.K.

GRIFFITHS, G.A. (1979) High sediment yields from major rivers of western Southern Alps, New Zealand. *Nature* 282: 61-63.

GROSSMAN G.D. (1982) Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. *American Naturalist* 119: 611-637.

GROSSMAN, G.D., M.C. FREEMAN, P.B. MOYLE, & J.O. WHITTAKER Jr. (1982) Stochasticity and assemblage organization in an Indiana stream fish assemblage. *American Naturalist* 126: 275-285.

GURTZ, M.E., G.R. MARZOLF, K.T. KILLENBECK, D.L. SMITH, & J.V. McARTHUR. (1988) Hydrologic and riparian influences on the import and storage of coarse particulate organic matter in a prairie stream. *Canadian Journal of Fisheries & Aquatic Sciences* 45: 655-665.

HAMILTON, A.L. (1969) On estimating annual production. *Limnology and Oceanography* 14: 771-782.

HARRISON, G.W. (1979) Stability under environmental stress: resistance, resilience, persistence and variability. *American Naturalist 113*: 659-669.

HART, D.D. (1983) The importance of competitive interactions within stream populations and communities. p.99-136. *In* Stream Ecology: Application and Testing of General Ecological Theory. Ed. by Barnes, J.R. & G.W. Minshall. Plenum, New York, U.S.A.

HERBOLD, B. (1984) Structure of an Indiana stream fish association: choosing an appropriate model. *American Naturalist 124*: 561-572.

HILDREW, A.G. (1986) Aquatic insects: patterns in life history, environment and community structure. p. 35-45. *In* Proceedings of the 3rd European Congress of Entomology.

HILDREW, A.G. & C.R. TOWNSEND. (1987) Organization in freshwater benthic communities. p. 347-371. *In* Organization of Communities: Past and Present. Ed. by Gee, J.H.R. & P.S. Giller. Blackwell Scientific Publications, Oxford, Great Britain.

HOLLING, C.S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics 4*: 1-23.

HOPKINS, C.L. (1976) Estimates of biological production in some stream invertebrates. *New Zealand Journal of Marine and Freshwater Research* 10: 629-640.

HUGHES, J.M.R. (1987) A study of riverine plant communities in Tasmania, with especial reference to central east coast rivers. Unpublished Ph.D. thesis, University of Tasmania, Hobart, Australia.

HYNES, H.B.N. (1970) The Ecology of Running Waters. Liverpool Press, Liverpool, U.K.

HYNES, H.B.N. (1970) The Ecology of Running Waters. Liverpool Press, Liverpool, U.K.

HYNES, H.B.N. (1975) The stream and its valley. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie* 19: 1-15.

JOERN, A. & K.P. PRUESS. (1986) Temporal constancy in grasshopper assemblies. *Ecological Entomology* 11: 379-385.

KEDDY, P.A. (1983) Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. *Ecology* 64: 331-344.

KEDDY, P.A. (1984) Plant zonation on lakeshores in Nova Scotia: a test of the resource specialization hypothesis. *Journal of Ecology* 72: 797-808.

KEITHAN, E.D. & R.L. LOWE. (1985) Primary productivity and spatial structure of phytolithic growth in streams in the Great Smoky Mountains National Park, Tennessee. *Hydrobiologia* 123: 59-67.

KREBS, C.J. (1985) Ecology. The experimental analysis of distribution and abundance. 3rd edition. Harper & Row, New York, U.S.A.

KRUEGER, C.C. & T.F. WATERS. (1983) Annual production of macro-invertebrates in three streams of different water quality. *Ecology* 64: 840-850.

LAKE, P.S. (1986) Stream communities and the management of streams. p. 3-21. *In* Stream Protection: the Management of Rivers for Instream Uses. Ed. by Campbell, I.A.C. Water Studies Centre, Caulfield Institute of Technology, Australia.

LAKE, P.S. & L.A. BARMUTA. (1986) Stream benthic communities: persistent presumptions and speculations. p. 263-276. *In* Limnology in Australia. Ed. by De Deckker, P. & W.D. Williams. CSIRO/Dr W. Junk, Dordrecht, The Netherlands.

MACAN, T.T. (1963) Freshwater Ecolgy. J. Wiley and Sons, New York, U.S.A.

MacARTHUR, R.H. (1955) Fluctuations of animal populations and a measure of community stability. *Ecology* 36: 533-536.

MacARTHUR, R.H. (1964) Environmental factors affecting bird species diversity. *American Naturalist* 98: 387-397.

MacARTHUR, R.H. (1969) Pattern of communities in the tropics. *Biological Journal of the Linnean Society* 1: 19-30.

MacARTHUR, R.H. & R. LEVINS. (1964) Competition, habitat selection, and character displacement in a patchy environemnt. *Proceedings of the National Academy of Sciences (USA)* 51: 1207-1210.

MacARTHUR, R.H. & J.W. MacARTHUR. (1961) On bird species diversity. *Ecology* 42: 594-598.

MACIOLEK, J.A. (1962) Limnological organic analyses by quantitative dichromate oxidation. U.S. Fisheries & Wildlife Service, *Research Report 61.*

MACKERETH, F.H.J. (1963) Some methods of water analysis for limnologists. Freshwater Biological Association, *Scientific Publication No. 21.*

MAY, R.M. (1972) Will a large complex system be stable? *Nature* 238: 413-414.

McAULIFFE, J.R. (1983) Competition, colonization patterns and disturbance in stream benthic communities. p. 137-156. *In* Stream Ecology. Applications and Testing of General Ecological Theory. Ed. by Barnes, J.R. & G.W. Minshall. Plenum, New York, U.S.A.

McAULIFFE, J.R. (1984) Resource depression by a stream herbivore: effects on distribution and abundances of other grazers. *Oikos* 42: 327-333.

McCAMMON, R.G. (1978) Organic energy flow in a mountain beech forest stream ecosystem. Unpublished M.Sc. thesis, University of Canterbury, Christchurch, New Zealand.

McELRAVY, E.P., G.A. LAMBERTI, & V.H. RESH. (ms) Influence of hydrologic regimes on annual variability of a stream macro-invertebrate community.

McFARLANE, A.G. (1951) Caddisfly larvae (Trichoptera) of the family Rhyacophilidae. *Records of the Canterbury Museum* 5: 267-289.

McINTOSH, R.P. (1980) The background and some current problems of theoretical ecology. *Synthese* 43: 195-225.

McNAUGHTON, S.J. (1988) Diversity and stability. *Nature* 333: 204-205.

MEFFE, G.K. & W.L. MINCKLEY. (1986) Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran desert stream. *American Midland Naturalist* 117: 177-191.

MENGE, B.A. (1976) Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* 46: 355-393.

MENGE, B.A. & J.P. SUTHERLAND. (1976) Species diversity gradients: synthesis of roles of predation, competition and temporal heterogenity. *American Naturalist* 110: 351-369.

MICHAELIS, F.B. (1973) The distribution and life history of *Rakiura vernale* (Trichoptera: Helicopsychidae). *Journal of the Royal Society of New Zealand* 3: 295-304.

MICHAELIS, F.B. (1974) The ecology of Waikoropupu Springs. Unpublished Ph.D. thesis, University of Canterbury, Christchurch, New Zealand.

MINCKLEY, W.L. (1963) The ecology of a spring stream: Doe Run, Meade County, Kentucky. *Wildlife Monographs* 11: 1-124.

MINSHALL, G.W. & R.C. PETERSEN. (1985) Towards a theory of macro-invertebrate community structure in stream ecosystems. *Archiv fur Hydrobiologie* 104: 49-76.

MOLLES, J.C. (1985) Recovery of a stream invertebrate community from a flash flood in Tesuque Creek, New Mexico. *The Southwestern Naturalist* 30: 279-287.

MOSS, B. (1967a) A spectrophotometric method for the estimation of percentage degradation of chlorophylls to phaeo-pigments in extracts of algae. *Limnology and Oceanography* 12: 335-340.

MOSS, B. (1967b) A note on the estimation of chlorophyll *a* in freshwater algal communities. *Limnology and Oceanography* 12: 340-342.

MUELLER, K. (1974) Stream drift as a chronological phenomenon in running water ecosystems. *Annual Review of Ecology and Systematics* 5: 309-323.

MULHOLLAND, P.J., J.W. ELWOOD, A.V. PALUMBO, & R.J. STEVENSON. (1986) Effect of stream acidification on periphyton composition, chlorophyll and productivity. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1846-1858.

NELSON, D.J. & D.C. SCOTT. (1962) Role of detritus in the productivity of a rock-outcrop community in a piedmont stream. *Limnology and Oceanography* 7: 396-413.

NEVES, R.J. (1979) Secondary production of epilithic fauna in a woodland stream. *American Midland Naturalist* 102: 209-224.

NEWELL, R.I.E. (1982) An evaluation of the wet oxidation technique for use in determining the energy content of seston samples. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1383-1388.

NEW ZEALAND METEROLOGICAL SERVICE (1987) Meterological Observations for 1976-1986. *Miscellaneous Publication* 109.

ORIANS, G.H. (1974) Diversity, stability and maturity in natural ecosystems. p. 139-150. *In* Unifying Concepts in Ecology. Ed. by van Dobben, W.H. & R.H. Lowe-McDonnell. Junk, The Hague, the Netherlands.

PAINE, R.T. (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal competitor. *Oecologia* 45: 93-120.

PATRICK, R., N.A. ROBERTS, & B. DAVIS. (1968) The effect of changes in pH on the structure of diatom communities. *Notulae Natura Academy of Natural Sciences (Philadelphia)* 416: 1-15.

PECKARSKY, B.L. (1983a) Biotic interactions or abiotic limitations? A model of lotic community structure. p. 303-323. *In* Dynamics of Lotic Ecosystems. Ed. by Fontaine III, T.D. & S.M. Bartell. Ann Arbor Scientific Publications, Michigan, U.S.A.

PECKARSKY, B.L. (1983b) The use of behavioural experiments to test ecological theory in streams. p. 79-98. *In* Stream Ecology. Applications and Testing of General Ecological Theory. Ed. by Barnes, J.R. & G.W. Minshall. Plenum, New York, U.S.A.

PFANKUCH, D.J. (1975) Stream reach inventory and channel stability evaluation. U.S.D.A. Forest Service, Region 1, Missoula, Montana, U.S.A.

PIANKA, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100: 33-46.

PIANKA, E.R. (1976) Competition and niche theory. p. 114-141. *In* Theoretical Ecology. Ed. by May, R.M. W.B. Saunders, Philadelphia, Pennsylvania, U.S.A.

PICKETT, S.T.A. & P.S. WHITE. (1985) The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, Florida, U.S.A.

PIMM, S.L. (1984) The complexity and stability of ecosystems. *Nature* 307: 321-326.

POULSEN, T.L. & D.C. CULVER. (1969) Diversity in terrestrial cave communities. *Ecology* 50: 153-158.

RAE, J.G. (1987) The effects of flooding and sediments on the structure of a stream midge assemblage. *Hydrobiologia* 144: 3-10.

RAHEL, F.J., J.D. LYONS, & P.A. COCHRAN. (1984) Stochastic or deterministic regulation of assemblage structure? It may depend on how the assemblage is defined. *American Naturalist* 124: 583-589.

REICE, S.R. (1984) The impact of disturbance frequency on the structure of a lotic riffle community. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie* 22: 1906-1910.

REICE, S.R. (1985) Experimental disturbance and maintenance of species diversity in a stream community. *Oecologia (Berl.)* 67: 90-97.

RESH, V.H. (1979) Sampling variability and life history features: basic considerations in the design of aquatic insect studies. *Journal of the Fisheries Research Board of Canada* 36: 290-311.

RICHARDSON, J.L. (1980) The organismic concept: resilience of an embattled ecological concept. *BioScience* 30: 465-471.

RICKER, W.E. (1946) Production and utilization of fish populations. *Ecological Monographs* 16: 373-391.

ROBINSON, C.T. & G.W. MINSHALL. (1986) Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *Journal of the North American Benthological Society* 5: 237-248.

ROSS,S.T., W.J. MATTHEWS, & A.A. ECHELLES. (1985) Persistence of stream fish assemblages: effects of environmental change. *American Naturalist* 126: 24-40.

ROUNICK, J.S. (1982) An investigation of carbon pathways in New Zealand streams. Unpublished Ph.D. thesis, University of Canterbury, Christchurch, New Zealand.

ROUNICK, J.S. & S.V. GREGORY. (1981) Temporal changes in periphyton standing crop during an unusually dry winter in streams of the Western Cascades, Oregon. *Hydrobiologia* 83: 197-205.

ROUNICK J.S. & M.J. WINTERBOURN. (1982) Benthic faunas of forested streams and suggestions for their management. *New Zealand Journal of Ecology* 5: 140-150.

ROUNICK, J.S. & M.J. WINTERBOURN. (1983a) Leaf processing in two contrasting beech forest streams: effects of physical and biotic factors on litter breakdown. *Archiv fur Hydrobiologie* 96: 448-474.

ROUNICK, J.S. & M.J. WINTERBOURN. (1983b) The formation, structure and utilization of stone surface organic layers in two New Zealand streams. *Freshwater Biology* 13: 57-72.

RYDER, G.I. (1983) Aquatic survey of two experimental catchment sites at Glendhu State Forest. New Zealand Forest Service/ Southland Conservancy.

SAGAR, P.M. (1983) Invertebrate recolonisation of previously dry channels in the Rakaia River. *New Zealand Journal of Marine and Freshwater Research* 17: 377-386.

SAGAR, P.M. (1986) The effects of floods on the invertebrate fauna of a large, unstable, braided river. *New Zealand Journal of Marine and Freshwater Research* 20: 37-46.

SANDERS, H.L. (1969) Benthic marine diversity and the stability-time hypothesis. *Brookhaven Symposium on Biology* 22: 71-80.

SCHOENER, T.W. (1974) The species-area relation within archipelagos: models and evidence from island land birds. *In* Proceedings of the International Ornithological Congress 16: 629-642.

SCRIMGEOUR, G.J. (1987) Effects of flood events on the benthic ecology of the Ashley, an unstable, North Canterbury river. Unpublished M.Sc. thesis, University of Canterbury, Christchurch, New Zealand.

SCRIMGEOUR, G.J., R.J. DAVIDSON & J.M. DAVIDSON. (1988) Recovery of benthic macro-invertebrate and epilithic communities following a large flood. *New Zealand Journal of Marine and Freshwater Research* 22: 337-344.

SCRIMGEOUR, G.J. & M.J. WINTERBOURN. (in press) Effects of floods on epilithon and benthic macro-invertebrate populations in an unstable New Zealand river. *Hydrobiologia.*

SHELDON, A.L. (1984) Colonization dynamics of aquatic insects. p. 401-429. *In* The Ecology of Aquatic Insects. Ed. by Resh, V.H. & D.M. Rosenberg. Praeger, New York, N.Y.

SIEGEL, S. (1956) Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill, New York, U.S.A.

SIEGFRIED, C.A. & A.W. KNIGHT. (1977) The effects of a washout in a Sierra foothill stream. *American Midland Naturalist* 98: 200-206.

SOUSA, W.P. (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15: 353-391.

SOUTHWOOD, J.R.E. (1988) Tactics, strategies and templets. *Oikos* 52: 3-18.

STANFORD, J.A. & J.V. WARD. (1983) Insect species diversity as a function of environmental variability and disturbance in stream ecosystems. p. 265-278. *In* Stream Ecology. Application and Testing of General Ecological Theory. Ed. by Barnes, J.R. & G.W. Minshall. Plenum, New York.

SWEENEY, B.W. (1984) Factors influencing life history patterns in aquatic insects. p. 56-100. *In* The Ecology of Aquatic Insects. Ed. by Resh, V.H. & D.M. Rosenberg. Praeger, New York, U.S.A.

SYKES, J.B. (Ed.) (1984) The Concise Oxford Dictionary of Current English. ($7^{th}$ edition). Oxford University Press, Oxford, U.K.

THURMAN, E.M. (1985) Organic Geochemistry of Natural Waters. $2^{nd}$ ed. Martinus Nijhoff/ Dr. W. Junk, Dordrecht, The Netherlands.

TOKESHI, M. (1986) Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. *Journal of Animal Ecology* 55: 491-506.

TOWNS, D.R. (1976) Dynamics of benthic invertebrate communities in a northern New Zealand kauri forest stream ecosystem. Unpublished Ph.D. thesis, University of Auckland, Auckland, New Zealand.

TOWNS, D.R. (1979) Composition and zonation of benthic invertebrate communities in a New Zealand kauri forest stream. *Freshwater Biology* 9: 251-262.

TOWNS, D.R. (1981) Life histories of benthic invertebrates in a kauri forest stream in northern New Zealand. *Australian Journal of Marine and Freshwater Research* 32: 191-211.

TOWNS, D.R. (1983a) A revision of the genus *Zephlebia* (Ephemeroptera: Leptophlebiidae). *New Zealand Journal of Zoology* 10: 1-52.

TOWNS, D.R. (1983b) Life history patterns of six sympatric species of Leptophlebiidae (Ephemeroptera) in a New Zealand stream and the role of interspecific competition in their evolution. *Hydrobiologia* 99: 37-50.

TOWNS, D.R. & W.L. PETERS. (1979) Three new genera of Leptophlebiidae (Ephemeroptera) from New Zealand. *New Zealand Journal of Zoology* 6: 213-235.

TOWNSEND, C.R. (1980) The Ecology of Streams and Rivers. Studies in Biology No. 122. Edward Arnold, London, U.K.

TOWNSEND, C.R. & A.G. HILDREW. (1988) Patterns and processes in low-order acid streams. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie* 23.

TOWNSEND, C.R., A.G. HILDREW, & K. SCHOFIELD. (1987) Persistence of stream invertebrate communities in relation to environmental variability. *Journal of Animal Ecology* 56: 597-613.

WARD, J.V. & J.A. STANFORD. (1979) Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. *In* The Ecology of Regulated Streams. Ed. by Ward, J.V. & J.A. Stanford. Plenum, New York, U.S.A.

WARD, J.V. & J.A. STANFORD. (1983) The intermediate disturbance Ed. by Fontaine III, T.D. & S.M. Bartell. Ann Arbor Science, Ann Arbor Michigan, U.S.A.

WARDLE, P. (1979) Plants and Landscape in Westland National Park. National Parks Series Number 3. National Parks Authority, Wellington, New Zealand.

WATERS, T.F. (1977) Secondary production in inland waters. *Advances in Ecological Research* 10: 91-164.

WATERS, T.F. (1979) Influence of benthic life history upon the estimation of secondary production. *Journal of the Fisheries Research Board of Canada* 36: 1425-1430.

WEBB, L.J., J.G. TRACEY, & W.T. WILLIAMS. (1972) Regeneration and pattern in subtropical rainforests. *Journal of Ecology* 60: 675.

WEBSTER, J.R., J.B. WAIDE, & B.C. PATTEN. (1975) Nutrient recycling and the stability of ecosystems. p. 1-27. *In* Mineral cycling in southeastern ecosystems. Ed. by Howell, F.G., J.B. Gentry, & M.H. Smith. Energy Research and Development Administration Symposium Series, Technical Information Center, Oak Ridge, Tennessee, U.S.A.

WETZEL, R.G. (1975) Limnology. W.B.Saunders Co., Philadelphia, Pennsylvania.

WIENS, J.A. (1974) Habitat heterogeneity and avian community structure in North American grasslands. *American Midland Naturalist* 91: 195-213.

WIENS, J.A. (1977) On competition and variable environments. *American Scientist* 65: 590-597.

WIENS, J.A. (1984) on understanding a non-equilibrium world: myth and reality in communitypatterns and processes. p. 439-457. *In* Ecological Communities: Conceptual Issues and the Evidence. Ed. by Strong Jr, D.R., D. Simberloff, L.G. Abele & A.B. Thistle. Princeton University Press, Princeton, New Jersey, U.S.A.

WIENS, J.A. & J.T. ROTENBERRY. (1980) Bird community structure in cold shrub deserts: competition or chaos? *In* Proceedings of the International Ornithological Congress (Berlin) 17: 1063-1070.

WILLIAMS, D.D. & I.D. HOGG. (1988) Ecology and production of invertebrates in a Canadian coldwater spring-springbrook system. *Holarctic Ecolgy* 11: 41-54.

WINTERBOURN, M.J. (1974) The life histories, trophic relations and production of *Stenoperla prasina* (Plecoptera) and *Deleatidium* sp. (Ephemeroptera) in a New Zealand river. *Freshwater Biology* 4: 507-524.

WINTERBOURN, M.J. (1978) The macroinvertebrate fauna of a New Zealand forest stream. *New Zealand Journal of Zoology* 5: 157-169.

WINTERBOURN, M.J. (1982) The invertebrate fauna of a forest stream and its association with fine particulate matter. *New Zealand Journal of Marine and Freshwater Research* 16: 271-281.

WINTERBOURN, M.J. (1986) Invertebrate communities. p167- 190. *In* Inland Waters of New Zealand. Ed. by Viner, A.B. DSIR Bulletin 241. DSIR, Wellington, New Zealand.

WINTERBOURN, M.J. & K.J. COLLIER. (1987) Distribution of benthic invertebrates in acid, brownwater streams in the South Island of New Zealand. *Hydrobiologia* 153: 277-286.

WINTERBOURN, M.J., K.J. COLLIER, & A.K. GRAESSER. (1988) Ecology of small streams on the west coast of the South Island, New Zealand. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie* 23.

WINTERBOURN, M.J. & K.L.D. GREGSON. (1981) Guide to the Aquatic Insects of New Zealand. *Bulletin of the Entomological Society of New Zealand* 5.

WINTERBOURN, M.J. & J.S. ROUNICK. (1985) Benthic faunas and food resources of insects in small New Zealand streams subjected to different forestry practices. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie* 22: 2148-2152.

WINTERBOURN, M.J., J.S. ROUNICK, & B. COWIE. (1981) Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* 15: 321-328.

YANT, P.R., J.R. KARR & P.L. ANGERMEIER. (1984) Stochasticity in stream fish communities: an alternative hypothesis. *American Naturalist* 124: 573-582.

YODZIS, P. (1978) Competition for Space and the Structure of Ecological Communities. (Lecture notes in biomathematics, 25.) Springer-Verlag, New York, U.S.A.

# APPENDIX ONE

## INTRODUCTION

Stream ecosystems are dependent on their terrestrial environment for sources of energy and nutrients in the form of dissolved and suspended material. Productivity of the stream community reflects the utilization of the resources by the stream community and is modified by the physical conditions of the stream. Streams have been classified on the basis of stability of selected physical conditions which reflect the capacity of the stream to adjust to and recover from environmental perturbation.

This survey was carried out for the NZ Forest Service and examined the broad-scale patterns between physico-chemical parameters and stream invertebrates of South Westland. Results presented here extend the findings of the intensive study of 4 streams to include both brownwater and clearwater streams in this region.

## METHODS

Surveys of 23 streams between Franz Josef Glacier and Haast were undertaken on 10-11 May and 18-19 August, 1985. Map references are given for each site in Table 1. Sites were chosen in catchments where no man-induced disturbances were apparent except for sites 4, 6, 8, 9 and 10 where some clearing of the catchments has occurred.

Physical conditions of the sites were compared using a survey procedure outlined by Pfankuch (1975) to evaluate stream stability in the U.S.A. This method has been used previously in New Zealand by Rounick & Winterbourn (1982). The technique evaluates the physical conditions of the 3 regions of the stream channel - upper banks, lower banks and streambed, producing an index which reflects the capacity of the stream to adjust to and recover from potential changes in flow and/or sediment

production (Pfankuch, 1975). High scores indicate low stability of the stream reach examined.

At each site, selected physico-chemical parameters - pH, alkalinity, conductivity and temperature of the stream water, were also measured. Channel slope and order were determined from topographical maps (N.Z. Topographic Map Series 1:63,360).

Stream invertebrates were collected using a 5 minute kick/sweep procedure with a pond net of 150 um mesh in all types of habitat present at each site. This qualitative sampling method is recommended for stream survey work where a comprehensive list of invertebrate taxa with a minimum of sampling effort is required (Elliott 1977). Stream invertebrates were collected from 17 of the 23 sites as some of the sites were situated on rivers too large to be sampled adequately using this method. Only twelve sites could be sampled in August due to high flows experienced while the survey was being carried out.

Table 1. Map references for 23 survey sites between Franz Josef Glacier and Haast (latitude,longitude)

| | | | |
|---|---|---|---|
| 1 | Smithys Ck | 43°23'30" | 170°07'30" |
| 2 | O'Connors Ck. | 43°24'30" | 170°06'20" |
| 3 | Small creek | 43°24'30" | 170°05'55" |
| 4 | Omoeroa R. | 43°24'20" | 170°05'45" |
| 5 | Small creek | 43°25'30" | 170°05'20" |
| 6 | Ohinetamatea R. | 43°29'25" | 169°54'10" |
| 7 | Black Ck. | 43°30'15" | 169°52'10" |
| 8 | MaiMai Ck. | 43°34'35" | 169°47'55" |
| 9 | Pita Ck. | 43°33'40" | 169°42'00" |
| 10 | Jacobs R. | 43034'20" | 169040'55" |
| 11 | Small creek | 43036'40" | 169035'05" |
| 12 | Makatata Ck. | 43037'25" | 169035'15" |
| 13 | Mahitahi R. | 43038'20" | 169035'00" |
| 14 | Paringa R. | 43042'40" | 169029'30" |
| 15 | Cedar Ck. | 430F4'45" | 169023'50" |
| 16 | Trib. Windbag | 43 46'20" | 169022'20 |
| 17 | Mimi Ck. | 43046'30" | 169 20'50" |
| 18 | Whakapohai R. | 43043'29" | 169014'45" |
| 19 | Venture Ck. | 43043'15" | 169014'30" |
| 20 | Grant Ck. | 43044'50" | 169010'55" |
| 21 | Cole Ck. | 43044'30" | 169010'25" |
| 22 | Ship Ck. | 43045'20" | 169009'00" |
| 23 | Waita R. | 43047'20" | 169007'30" |

(i) Analysis of Faunal Results

Hierarchial classification techniques have been used to produce groups or clusters of related samples based on their taxonomic composition. A sample by sample dissimilarity matrix was computed using (1 - Sorensen's index of similarity) as a dissimilarity measure (Sorensen 1948). Sorensen's index compares the invertebrate composition of 2 samples (A & B) using the following formula:

$$C_S = 2j/(a + b).$$

where j is the number of taxa common to samples A and B,

a is the number of taxa present in sample A, and

b is the number of taxa present in sample B.

Three clustering procedures were used:

(1) complete linkage clustering, where dissimilarity between groups or clusters of samples is equal to the maximum dissimilarity within clusters (Sorensen 1948),

(2) average linkage clustering, where where dissimilarity between groups or clusters of samples is equal to the average dissimilarity within groups (Sokal & Michener 1958), and

(3) minimum linkage clustering, which groups clusters or samples so that the increase in within cluster variance is less than it would be if either of the clusters or samples were joined with any other cluster (Ward 1963).

Canonical discriminant and canonical correlations analysis were used to interpret the environmental data in relation to the stream clusters and their major taxa. Canonical discriminant analysis finds linear combinations physico-chemical parameters that best explain the differences among stream clusters (Fisher 1936). Canonical correlation

analysis explains or summarizes the relationships between 2 sets of variables (physico-chemical parameters & presence/absence data of most frequently occurring taxa in clusters) by finding a small number of linear combination from each set that account for the most variance between the sets of variables (Hotelling 1936). Both require within class distributions to be approxiamately normal; results can still used descriptively with non-normal data.

Results and Interpretation:

(i) Physico-chemical parameters

Physico-chemical data are presented in Table 2. Stream water temperatures were between 7 and 12.5 °C. Most sites had acidic stream water (pH 4.8-6.9) except for 3 sites which were slightly alkaline (pH > 7). Lowest pH was recorded at O'Connors Creek in August. Conductivity at most sites ranged between 11 and 88 uS/cm (at 25 °C) in both surveys. In May, markedly higher conductivities were recorded at sites 19 and 21. Alkalinity concentrations ranged from 0.38 to 17.16 mg $CaCO_3$/l and generally were higher in May than August. Alkalinity levels reflect the buffering capacity of the stream water and lower values recorded in August reflected the recent heavy rainfall and subsequent high flows experienced while the survey was being carried out.

Table 2: Physico-chemical data collected from 23 sites in South Westland surveyed in May and August, 1985

| Site | Month | Temp. (°C) | pH | Cond. ($\mu s.cm^{-1}$) at 25°C | Alk. ($mgCaCO_3/\ell$) | Order | Slope[1] (°) | Stab. * |
|---|---|---|---|---|---|---|---|---|
| 1. Smithys Ck. | M | - | 6.5 | 86.5 | 7.58 | 1 | 12 | 88 |
| | A | 7.5 | 6.3 | 34.2 | 3.0 | | | |
| 2. O'Connors Ck. | M | 7.0 | 5.83 | 11.4 | 0.56 | 2 | 0 | 71 |
| | A | 7.0 | 4.8 | 14.5 | 0.38 | | | |
| 3. Small Creek | M | - | 6.0 | 37.5 | 3.14 | 1 | 0 | 75 |
| | A | 8.5 | 6.1 | 25.0 | 1.75 | | | |
| 4. Omoeroa R. | M | - | 6.8 | 85.7 | 7.87 | 3 | 0 | 102 |
| | A | 7.0 | 6.6 | 53.2 | 4.2 | | | |
| 5. Small Creek | M | - | 6.5 | 72.7 | 6.31 | 1 | 58 | 62 |
| | A | 7.5 | 6.9 | 84.5 | 7.11 | | | |
| 6. Ohinetamatea R. | M | - | - | 68.0 | 4.3 | 3 | 0 | 95 |
| | A | 9.5 | 6.3 | 36.0 | 2.36 | | | |
| 7. Black Ck. | M | 8.5 | 5.8 | 33.2 | 2.3 | 2 | 26 | 79 |
| | A | 7.0 | 6.2 | 24.5 | 0.998 | | | |
| 8. MaiMai Ck. | M | - | - | - | - | 2 | 0 | 121 |
| | A | 9.0 | 6.5 | 42.7 | 2.98 | | | |
| 9. Pita Ck. | M | 12.5 | 6.2 | 63.5 | 5.61 | 1 | 0 | 54 |
| | A | 9.0 | 5.95 | 51.2 | 3.42 | | | |
| 10. Jacobs R. | M | - | - | - | - | 3 | 0 | 124 |
| | A | 7.0 | 5.8 | 17.8 | 1.34 | | | |
| 11. Small Creek | M | 10.0 | 5.88 | 65.0 | 4.26 | 1 | 0 | 51 |
| | A | 9.0 | 6.2 | 44.0 | 2.94 | | | |
| 12. Makatata Ck. | M | 11.5 | 6.52 | 60 | 5.61 | 2 | 0 | 108 |
| | A | 11 | 6.25 | 56 | 4.44 | | | |
| 13. Mahitahi Ck. | M | 10 | 6.65 | 50.8 | 3.57 | 4 | 0 | - |
| | A | - | - | - | - | | | |
| 14. Paringa R. | M | - | - | - | - | 4 | 0 | 128.5 |
| | A | 9 | 5.85 | 25.7 | 2.0 | | | |
| 15. Cedar Ck. | M | 8.5 | 6.69 | 25.0 | 1.11 | 1 | 5 | 80 |
| | A | 9 | 5.95 | 21.5 | 0.96 | | | |
| 16. Trib. Windbag | M | 10 | 6.73 | 47.0 | 4.26 | 1 | 0 | 110 |
| | A | 9.5 | 5.8 | 15.7 | 0.61 | | | |
| 17. Mimi Ck. | M | 9 | 6.92 | 37.4 | 3.67 | 1 | 19 | 55 |
| | A | 8.5 | 5.7 | 15.5 | 0.72 | | | |
| 18. Whakapohai R. | M | 10 | 7.11 | 49.5 | 4.57 | 3 | 0 | 112 |
| | A | 9 | 6.5 | 26.2 | 1.21 | | | |
| 19. Venture Ck. | M | 11 | 7.55 | 175. | 17.16 | 1 | 10 | 61 |
| | A | 9.5 | 6.4 | 55.5 | 3.23 | | | |
| 20. Grant Ck. | M | 10 | 6.47 | 87.5 | 6.37 | 1 | 11 | 67 |
| | A | 9.5 | 6.25 | 43.1 | 1.15 | | | |
| 21. Cole Ck. | M | 10 | 7.26 | 143. | 16.7 | 3 | 0 | 64 |
| | A | 9 | 6.45 | 43.7 | 1.82 | | | |
| 22. Ship Ck. | M | 9 | 6.5 | 63.7 | 5.7 | 3 | 0 | 67 |
| | A | 9 | 6.3 | 58.5 | 3.44 | | | |
| 23. Waita R. | M | 9 | 6.5 | 37.9 | 3.19 | 4 | 0 | 100 |
| | A | 9 | 6.1 | 28.2 | 1.52 | | | |

* Stability scores 38-76 Good, 77-114 Fair, 115+ Poor

1. Slope values shown as 0 mean < 1°

Pfankuch stability ratings obtained for the 23 sites ranged from 51 to 129. Three sites - MaiMai Creek, and Jacobs and Paringa Rivers, had ratings greater than 115 which places them in Pfankuch's "poor" category, and indicates low resistance to physical disturbance. Nine sites had ratings between 77 and 114 and therefore "fair" resistance to disturbance and 10 sites were classified as "good" (< 77). Both Jacobs and Paringa Rivers are large and prone to flooding. Stream size presumably influences the resistive capacity of the stream channel and stream order (an index of stream size) was shown to be positively correlated with stability ratings (Table 3) ie. larger streams are less resistant to disturbance.

Data were analysed for possible relationships between physico-chemical parameters and stability ratings of each site (Table 3). Temperature, pH, conductivity and alkalinity were all positively correlated with each other. Stability was negatively correlated with stream order as indicated above although channel slope was negatively correlated with stream order.

**Table 3.** Spearman rank correlation coefficients for selected physico-chemical parameters measured at each site during May and August 1985 (* $p < 0.05$, ** $p < 0.01$).

| Parameters | Coefficients |
|---|---|
| pH - temperature | $r = 0.38$, $n = 42$ * |
| pH - conductivity | $r = 0.62$, $n = 42$ ** |
| pH - alkalinity | $r = 0.68$, $n = 42$ ** |
| Alk - conductivity | $r = 0.78$, $n = 42$ ** |
| Order - slope | $r = -0.52$, $n = 23$ * |
| Order - Pfankuch score | $r = 0.48$, $n = 23$ * |

(ii) Stream invertebrates - Composition and Distribution.

A list of taxa and their relative abundances at each site on each sampling trip are given in Table 4. In all, 4,540 invertebrates belonging to 78 recognizable taxonomic groups were collected. These included 20 taxa of Plecoptera, 6 Ephemeroptera, 1 Megaloptera, 15 Diptera, 27 Trichoptera, 4 Coleoptera and 5 other invertebrate taxa. Most of the invertebrates collected were insect nymphs and larvae. Four taxa - *Nesameletus* and *Deleatidium* (both mayfly nymphs), Chironomidae and Elmidae, were present in collections from most sites.

Highest numbers of taxa (species richness) were recorded from sites 3, 11, 19 and 20 where 32, 24, 30 and 27 taxa were identified, respectively. Only 4 or 5 taxa of invertebrates were recorded from sites 6, 15, 18 and 23, which were all sampled once only, however. The 4 sites with the highest species richness had between 6 and 15 trichopteran taxa compared to 0 or 1 at the 4 sites with the lowest species richness.

In May, sites 1-7, 9, 11, 16-21 and 23 were sampled for stream invertebrates, while sites 1-5, 9, 11, 15, 16 and 19-21 were sampled in August. Fewer sites were sampled in August because of the heavy rain and subsequent high flows experienced while the survey was being carried out. Species richness appeared to be similar between surveys except for sites 11 and 16 where twice as many taxa were collected in August. Further analysis will show whether these differences are biologically significant.

TABLE 4: List of taxa and their relative abundances at each site collected in May and August surveys.

| Site Number | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | 7 | 9 | | 11 | | 15 | 16 | | 17 | 18 | 19 | | 20 | | 21 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MAY | AUG | MAY | AUG | MAY | AUG | MAY | AUG | MAY | AUG | MAY | MAY | MAY | AUG | MAY | AUG | AUG | MAY | AUG | MAY | MAY | MAY | AUG | MAY | AUG | MAY | AUG | MAY |
| *Potamopyrgus antipodarum | - | - | - | - | 4.44 | 7.64 | - | - | - | - | - | - | - | - | 23.85 | 4.44 | - | 21.74 | 17.92 | - | - | 29.17 | - | - | - | - | 10.81 | - |
| Oligochaetes | - | - | - | 0.85 | - | - | - | - | - | - | - | - | - | 4.38 | - | - | 3.57 | - | - | - | - | - | 3.45 | - | - | - | - | - |
| Hydracarina | - | - | - | - | - | - | - | - | - | - | - | - | 2.38 | - | - | - | - | - | - | - | - | - | - | 1.92 | - | - | - | - |
| Amphipod | - | - | - | - | - | - | - | - | - | 6.06 | - | - | - | - | - | - | - | - | - | - | - | 4.17 | - | - | - | - | - | - |
| *Insect* nymph | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 39.19 | - |
| Stenoperla unident. | 0.21 | - | 0.21 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2.13 | - | - |
| Stenoperla prasina | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.74 | - | - | - | - | - | - | - | - | - | - | - | - |
| S. maclellani | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.74 | - | - | - | 1.10 | - | - | 3.45 | - | - | - | - | - |
| *Austroperla cyrene | - | - | - | - | - | - | - | - | 1.43 | 3.03 | - | - | - | - | 0.92 | 0.89 | - | - | 0.94 | - | - | 6.94 | 8.62 | 3.85 | - | 2.13 | - | - |
| Megaleptoperla grandis | - | - | - | - | - | - | - | - | 1.19 | - | - | 2.12 | - | - | - | - | - | - | - | - | - | - | - | 1.92 | - | - | - | - |
| M. diminuta | - | - | - | - | 0.30 | - | - | 0.57 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Zelandoperla unident. | - | 1.31 | - | - | - | - | - | 0.57 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Z. denticulata | - | - | - | - | - | - | - | - | 0.24 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.92 | 3.33 | - | - | - |
| Z. decorata | - | 1.04 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3.57 | - | - | - | - | - | - | 5.77 | - | - | - | - |
| Z. agnetis | 1.06 | - | - | - | 0.30 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6.59 | - | - | - | - | 20.0 | - | - | - |
| Zelandobius unident. | - | - | 0.41 | 5.08 | - | - | - | 0.57 | 0.24 | 3.03 | - | 2.65 | - | - | - | - | - | 2.17 | - | 3.30 | - | - | - | - | - | - | - | - |
| Z. confusus | 0.63 | 1.04 | 6.56 | - | 0.30 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2.78 | - | 1.92 | - | - | - | - |
| Z. furcillatus | - | - | - | - | 1.48 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.92 | - | - | - | - |
| Nesoperla sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Acroperla trivacuata | - | - | - | - | - | - | - | 0.57 | - | - | - | - | - | - | - | - | - | - | 0.94 | - | - | 1.39 | - | 3.85 | 16.67 | - | 13.51 | - |
| *Spaniocercoides sp. | 1.06 | 1.31 | 1.23 | 0.85 | - | - | - | - | 1.67 | - | - | 1.06 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cristaperla fimbria | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.15 | - | - | 2.83 | - | - | - | - | 1.92 | - | - | - | - |
| Halticoperla viridans | - | - | - | - | - | - | - | - | 0.24 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Spaniocerca zelandica | - | - | - | - | - | - | - | - | - | 6.06 | - | 0.53 | - | - | - | - | - | - | - | - | - | 1.39 | - | - | 3.33 | - | - | - |
| S. longicauda | - | 0.52 | - | - | - | - | - | 0.57 | - | 3.03 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Coloburiscus humeralis | - | - | - | 0.85 | 6.80 | 14.93 | - | - | - | - | - | - | - | - | - | - | - | - | 0.94 | - | - | 1.39 | - | - | - | - | - | - |
| *Nesameletus sp. | 3.6 | 3.41 | 1.64 | 0.85 | 2.66 | 3.82 | 1.34 | 10.57 | 1.43 | 3.03 | 1.77 | 2.12 | - | 0.63 | - | - | - | - | 1.89 | 10.99 | - | 4.17 | - | 19.23 | 3.33 | 2.13 | 1.35 | - |
| Ameletopsis sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.63 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Deleatidium sp. | 62.89 | 79.0 | 30.33 | 42.37 | 21.01 | 29.51 | 53.69 | 80.46 | 73.81 | 27.27 | 11.5 | 34.39 | - | 7.50 | 9.17 | 28.9 | 71.43 | - | 9.43 | 53.85 | 11.76 | 8.33 | 60.34 | 21.15 | 9.1 | 19.15 | 6.76 | - |
| Austroclima sp. | - | - | - | 0.85 | 5.62 | 10.76 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Maufulus sp. | 2.77 | - | - | - | - | 0.35 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Archichauliodes diversus | - | - | - | - | 2.37 | 1.74 | - | - | - | - | - | 4.76 | - | - | 0.92 | 1.19 | - | 4.35 | 0.94 | - | - | 1.39 | - | - | - | 4.26 | - | - |
| Neocurupira tonnoiri | 0.42 | 0.26 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.10 | - | - | - | - | - | - | - | - |
| M. campbelli | - | - | - | - | - | - | - | - | 0.48 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Zelandotipula sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Limonia sp. | - | - | - | - | - | - | - | - | - | 12.12 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Aphrophila sp. | - | 0.52 | - | - | 1.78 | 0.35 | - | - | - | - | - | - | - | - | 2.75 | 0.15 | - | - | - | - | - | - | 1.72 | - | - | - | - | - |
| Eriopterini sp. | 0.21 | 2.62 | - | - | - | - | - | 1.15 | - | - | - | - | - | - | - | 0.15 | - | - | - | - | - | - | - | - | - | - | - | 5.88 |
| *Paralimnophila skusei | - | - | - | - | - | - | - | - | 0.48 | 15.15 | - | - | - | - | - | 0.15 | - | 2.17 | - | - | 47.06 | - | 3.45 | - | 3.33 | - | 5.41 | - |
| Hexatomini sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3.33 | - | - | 5.88 |
| Austrosimulium sp. | - | - | - | - | 0.3 | 4.51 | - | - | 0.95 | 3.03 | - | 1.59 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2.7 | - |
| Psychodidae | - | - | - | - | - | - | - | - | - | 3.03 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Chironomidae | 37.31 | 4.19 | 45.08 | 6.78 | 26.33 | 4.17 | 14.09 | 5.17 | 11.43 | 9.09 | 82.3 | 41.8 | - | 27.50 | - | 3.85 | 14.29 | 67.39 | 32.08 | 4.40 | - | - | 3.45 | 3.85 | 23.34 | 10.64 | 4.05 | 64.71 |
| *Ceratopogonidae | - | - | 0.41 | - | 0.59 | 0.69 | - | - | - | - | - | - | 11.9 | 28.75 | - | - | - | - | 4.72 | - | - | - | - | - | - | - | - | 23.53 |
| Empididae | - | - | - | - | 2.07 | 0.70 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.72 | 1.92 | - | - | - | - |
| Ephydridae | - | - | 0.41 | - | - | - | - | - | - | - | - | 0.53 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Mycetophilidae | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3.33 | - | - | - |
| *Psilochorema sp. | - | - | 1.23 | 2.54 | 1.18 | 2.43 | 0.67 | - | - | - | - | - | - | 0.63 | 1.83 | - | - | - | - | - | 35.29 | - | 1.72 | - | - | - | - | - |
| Hydrobiosis unident. | 0.21 | 2.08 | 1.23 | - | - | - | 1.34 | - | 0.48 | - | - | - | - | - | - | - | - | - | - | 2.20 | - | - | - | - | 3.33 | - | - | - |
| H. silvicola | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.15 | - | - | - | - | - | - | - | 7.69 | - | - | - | - |
| *Costachorema unident. | - | - | - | 0.85 | 0.89 | 1.03 | - | - | 3.81 | 3.03 | 1.77 | - | - | 1.25 | - | 0.3 | 7.14 | - | - | - | - | - | - | 1.92 | - | - | - | - |
| C. psaroptera | - | 0.26 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| C. brachyptera | 0.63 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Edpercivalia sp. | - | - | - | - | - | - | - | - | - | - | - | - | 2.38 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Neurochorema sp. | 0.42 | - | 4.51 | 2.54 | 4.14 | 0.35 | - | - | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - |
| Hydrochorema tenuicaudatum | - | - | - | - | - | - | 0.67 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.72 | - | - | - | - | - |
| H. crassicaudatum | 0.42 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.72 | - | - | - | - | - |
| Polyplectropus sp. | - | - | - | - | 0.89 | 0.35 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Oxyethira albiceps | - | - | - | - | 3.85 | - | - | - | - | - | 2.65 | - | 2.38 | - | - | - | - | - | 15.09 | - | - | - | - | - | - | - | - | - |
| *Paroxyethira eatoni | - | - | - | - | 0.89 | - | - | - | - | - | - | - | - | - | 0.92 | - | - | - | 3.77 | - | - | - | - | - | - | 2.13 | - | - |
| *Aoteapsyche colonica | - | - | - | - | - | 0.35 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.39 | - | - | - | - | - | - |
| *Helicopsyche zelandica | - | - | - | - | - | 0.70 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.10 | - | 18.06 | 1.72 | 1.92 | - | 2.13 | - | - |
| *Philorheithrus agilis | - | - | 1.23 | - | - | - | - | - | - | - | - | - | - | - | 0.92 | 23.70 | - | 2.17 | - | - | - | 1.39 | - | 1.92 | - | 6.38 | 2.7 | - |
| Hudsonema aliena | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.39 | - | - | - | 2.13 | - | - |
| Triplectides obsoleta | - | - | - | - | 0.30 | - | - | - | - | - | - | - | 2.38 | - | 0.92 | - | - | - | - | - | - | - | 1.72 | - | - | - | - | - |
| Pycnocentrella eruensis | - | - | - | - | - | 0.35 | - | - | - | - | - | 0.53 | - | 4.38 | - | - | - | - | 1.89 | - | - | - | - | - | - | - | - | - |
| Zelolessica cheira | - | - | 0.82 | 25.42 | 0.30 | - | - | - | - | - | - | 3.17 | - | - | - | - | - | - | - | - | - | - | 1.72 | - | - | - | - | - |
| Pycnocentrodes aureola | - | - | - | - | 0.30 | - | - | - | - | - | - | - | 28.57 | 5.0 | 8.26 | 13.78 | - | - | - | 6.59 | - | 2.78 | - | 3.85 | - | 2.13 | - | - |
| Conuxia gunni | - | - | - | - | 1.78 | 3.12 | - | - | - | - | - | - | - | - | - | - | - | - | 0.94 | - | - | - | - | - | - | - | - | - |
| *Olinga feredayi | - | - | - | - | 7.99 | 12.15 | - | - | - | - | - | - | 2.38 | - | 8.26 | 4.74 | - | - | 0.94 | - | - | - | 1.72 | - | - | 2.13 | - | - |
| Pycnocentria evecta | - | - | - | - | - | - | - | - | - | - | - | 1.59 | 40.48 | - | 41.28 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| P. sylvestris | - | - | - | - | 0.89 | - | - | - | - | - | - | - | - | - | - | 14.96 | - | - | - | - | - | - | - | - | - | - | - | - |
| P. funerea | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.94 | - | - | - | - | - | - | - | - | - |
| Oeconesidae | - | - | - | - | - | - | - | - | 0.24 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Elmidae adults | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2.78 | - | - | - | - | - | - |
| *Elmidae larvae | 2.77 | 2.36 | 4.10 | 10.17 | 0.30 | - | 28.19 | 9.77 | 1.9 | 3.03 | - | 3.17 | 7.14 | 19.38 | - | - | - | - | - | 6.59 | 5.88 | 8.33 | 1.72 | 7.69 | - | 6.38 | - | - |
| Helodidae larvae | 0.21 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.15 | - | - | - | - | - | - | - | - | - | 36.17 | 9.46 | - |
| Staphylinidae adults | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2.20 | - | - | - | - | 3.33 | - | - | - |
| Hydrophilidae larvae | - | - | 0.41 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.39 | - | - | - | - | - | - |
| * adults | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.92 | - | - | - | - |
| Total no.s invertebrates | 469 | 381 | 244 | 118 | 338 | 288 | 149 | 174 | 420 | 33 | 113 | 189 | 42 | 160 | 109 | 675 | 28 | 46 | 106 | 91 | 17 | 72 | 58 | 52 | 30 | 47 | 74 | 17 |
| Total no.s taxa | 16 | 14 | 16 | 13 | 28 | 21 | 7 | 10 | 16 | 14 | 5 | 14 | 9 | 11 | 12 | 20 | 5 | 6 | 17 | 12 | 4 | 18 | 16 | 20 | 12 | 14 | 10 | 4 |

**Table 5.** Spearman rank correlation coefficients for species richness (total & Trichoptera) and Pfankuch stability index for 28 stream data sets (* $p < 0.05$, ** $p < 0.01$).

| | Total no. taxa | No. Trichopteran Taxa |
|---|---|---|
| Tot.stability score | r= -0.37 | r= -0.43 * |
| Lower banks score | r= -0.54 ** | r= -0.34 |
| Streambed score | r= -0.38 * | r= -0.52 ** |

Correlations between both species richness and numbers of trichopteran taxa identified and the Pfankuch stability index are shown in Table 5. The Trichoptera (caddisflies) were selected as their larvae show considerable specialization (Cowie, 1980). Total Pfankuch scores and scores for lowerbank and streambed stability (ie. sections of the survey procedure) were considered. Species richness was negatively correlated with scores for lower banks and streambed stability ie. more species occurred where stability was greater. Similarly, negative correlations were found between numbers of caddisfly taxa and scores of total stability and streambed stability.

(iii) Community Structure

Associations between the 28 collections of invertebrates were revealed using the 3 clustering procedures outlined earlier. The number of clusters and their compositions were very similar using the different methods (Table 6).

trichopteran taxa and fewer plecopteran and ephemeropteran taxa than August samples.

Table 6. Composition of clusters obtained with 3 clustering methods. Collections identified by site number and survey trip (M= May, A= August)

| | Complete linkage method | Average linkage method | Ward's min.variance linkage method |
|---|---|---|---|
| 1 | 1M,1A,2M,2A,4A,7M,21A | 1M,1A,4A,17M,20A | 1M,1A,4A,17M,20A,21A |
| 2 | 5M,5A,17M,20A | 2M,2A,5M,5A,7M | 2M,2A,5M,5A,7M |
| 3 | 4M,9A,18M,19A | 4M,9A,18M,19A | 4M,6M,9A,15A,18M,19A |
| 4 | 6M,15A | 6M,15A | - |
| 5 | 9M | 9M | - |
| 6 | 3M,3A,11M,11A,16A | 3M,3A,11M,11A,16A | 3M,3A,9M,11M,11A,16A |
| 7 | 16M,23M | 16M,23M | 16M,23M |
| 8 | 19M,20M,21M | 19M,20M,21M | 19M,20M,21M |

Taxa that always occurred in each cluster of samples were used in a canonical correlation analysis of the physico-chemical data of the samples. Taxa are marked with an asterisk in Table 4. Correlation coefficients between physico-chemical parameters and frequency of occurrence of taxa (presence absence data) are presented in Table 7. Relationships were considered to be important when the coefficient value was greater than 0.3.

Three groups of taxa were defined in this way.

Group 1 - *Austroperla cyrene, Archichauliodes diversus, Aoteapsyche colonica, Helicopsyche poutini* and *Philorheithrus agilis*, were positively associated with some water chemistry parameters but negatively correlated with stream order, slope and stability scores.

Group 2 - *Spaniocercoides*, Chironomidae, Ceratopogonidae, *Psilochorema*, *Costachorema* and *Neurochorema*, were negatively correlated with water chemistry parameters such as pH, conductivity and alkalinity levels.

Group 3 - the remaining 10 taxa showed no consistent relationships with any physico-chemical parameters.

Table 7. Correlations between the most frequently occurring taxa in the cluster groups and physico-chemical parmeters measured from 23 sites surveyed in May and August, 1985.

| | Temp | pH | Cond | Alk | Order | Slope | Stab. Score |
|---|---|---|---|---|---|---|---|
| *A. colonica* | 0.28 | 0.41 | 0.46 | 0.26 | -0.17 | -0.09 | -0.33 |
| *A. cyrene* | -0.22 | -0.24 | 0.52 | 0.31 | -0.31 | 0.29 | -0.38 |
| *A. diversa* | 0.28 | 0.00 | 0.20 | 0.04 | -0.23 | -0.21 | -0.03 |
| *H. poutini* | 0.35 | 0.25 | 0.42 | 0.19 | -0.10 | -0.25 | -0.27 |
| *P. agilis* | 0.10 | 0.33 | 0.52 | 0.26 | 0.13 | -0.17 | -0.19 |
| Chironomidae | -0.61 | -0.24 | -0.37 | -0.48 | 0.06 | 0.20 | 0.14 |
| Ceratopogonidae | 0.11 | -0.34 | -0.30 | -0.25 | -0.04 | -0.28 | 0.02 |
| *Costachorema* sp. | -0.23 | -0.34 | -0.28 | -0.14 | -0.23 | 0.26 | -0.24 |
| *Neurochorema* sp. | -0.32 | -0.42 | -0.23 | -0.22 | -0.22 | -0.22 | -0.17 |
| *Psilochorema* sp. | -0.20 | -0.35 | -0.19 | -0.17 | 0.02 | -0.34 | -0.05 |
| *Spaniocercoides* sp. | -0.55 | -0.40 | -0.17 | -0.11 | -0.08 | 0.35 | 0.01 |
| *Aphrophila sp.* | *-0.06* | *-0.20* | *-0.19* | *-0.16* | *-0.08* | *-0.19* | *-0.08* |
| *Deleatidium* sp. | -0.42 | -0.07 | 0.04 | -0.03 | -0.13 | 0.17 | -0.22 |
| Elmidae | -0.22 | 0.20 | 0.39 | 0.31 | 0.06 | 0.26 | -0.21 |
| *Nesameletus* sp. | -0.45 | -0.01 | 0.11 | 0.08 | 0.01 | 0.28 | -0.04 |
| *O. feredayi* | *0.01* | *-0.26* | *-0.26* | *-0.23* | *-0.24* | *-0.17* | *0.19* |
| *P. antipodarum* | *-0.26* | *-0.03* | *0.04* | *0.08* | *-0.27* | *-0.31* | *-0.05* |
| *P. aureola* | 0.34 | -0.28 | -0.02 | -0.03 | -0.32 | -0.23 | -0.47 |
| *P. eatoni* group | *0.29* | *-0.04* | *0.21* | *0.28* | *-0.28* | *-0.20* | *-0.04* |
| *P. skusei* | *0.04* | *0.24* | *0.00* | *0.01* | *-0.01* | *0.34* | *0.07* |
| *Z. chiera* | -0.02 | -0.07 | 0.20 | 0.04 | -0.06 | -0.06 | -0.36 |

Canonical correlation analysis determines how much of the variance between physico-chemical data and presence/absence of taxa data can be accounted for by the linear combinations from each set of variables (Table 8). The first 2 canonical correlations accounted for 54 percent of the total variance of the combined data set. However, the first

Canonical correlation analysis determines how much of the variance between physico-chemical data and presence/absence of taxa data can be accounted for by the linear combinations from each set of variables (Table 8). The first 2 canonical correlations accounted for 54 percent of the total variance of the combined data set. However, the first canonical correlation had a value of unity which usually indicates that the variables concerned are correlated. This was so as shown in Table 3, and as a result interpretation becomes more difficult, because no significance values for the correlations can be reliably calculated (Gittins, 1979).

**Table 8.** Cumulative percentage of variance of total combined data, physico-chemical data and taxon data, accounted for by the canonical correlations.

| | Canonical Correlation | Cumulative percent of variance | | | Signif. |
|---|---|---|---|---|---|
| | | Total data | Phy/chem. | Taxa | |
| 1 | 1.0000 | - | 10.93 | 5.83 | p= 0.00 |
| 2 | 0.9763 | 54.33 | 30.09 | 13.72 | p= 0.05 |
| 3 | 0.9391 | 73.00 | 42.50 | 17.92 | NS |
| 4 | 0.9240 | 88.29 | 59.90 | 27.41 | NS |

Nevertheless, these results can still provide useful biological insights as to the factors influencing stream community structure. The first canonical variable or axis of the taxon matrix was negatively correlated with stability scores and stream gradient, whereas the second was positively correlated with temperature, pH and conductivity of stream water. Since ten taxa used in this analysis showed no strong relationships with any physico-chemical parameters, it is not altogether surprising that the model accounted for only fourteen percent of the variation between invertebrate collections.

The first physico-chemical axis was correlated with the presence of *A. colonica* (filter feeding caddisfly larvae) and *H. poutini* (grazing caddisfly larvae) and the second axis was correlated with the presence of *A. cyrene* (stonefly nymph) and the absence of *Spaniocercoides* (stonefly nymph), *Psilochorema* and *Neurochorema* (both predatory caddisfly larvae). These axes accounted for thirty percent of the variance in physico-chemical data.

These results confirm the interpretations based on the correlation values presented in Table 7, where ten taxa were shown to be commonly present in the stream fauna regardless of physico-chemical conditions. Of these two mayfly nymphs - *Deleatidium* and *Nesameletus* and elmid beetle larvae, were also numerically abundant at most sites. Rounick & Winterbourn (1982) observed that a "common core" of stream invertebrates was found in streams of varying physico-chemical conditions. This was borne out by results of the South Westland stream survey.

**Table 9.** Cumulative percentage of variance in the physico-chemical data of the stream clusters accounted for by the canonical axes and their canonical correlations.

| Canonical axis | Associated with environ. factors | Canonical correl'n | Cumulative percentage of variance | Signif. |
|---|---|---|---|---|
| 1 | Temp, cond. & slope | 0.6810 | 67 | p= 0.09 |
| 2 | pH, order &s tability | 0.5429 | 100 | NS |

Canonical discriminant analysis was used to interpret the stream clusters based on faunal composition. Two discriminant functions based on a number of combined or related environmental parameters were obtained (Table 9). The first canonical axis was correlated strongly with temperature, conductivity and slope, whereas the second axis was made up

of a number of parameters - pH, stream order and stability. The first axis accounted for 67 percent of the total variance of the stream cluster, although the correlation value was not statistically significant (ie. $p > 0.05$).

## SUMMARY

Three aquatic insect genera - *Spaniocercoides*, *Psilochorema* and *Neurochorema*, were negatively associated with increasing pH, conductivity and temperature of stream water, whereas *A. cyrene*, *A. colonica* and *H. poutini*, were positively associated with high stream water alkalinity and conductivity. Caddisfly larvae with specialized feeding modes - algal grazers (*H. poutini*) and filter feeders (*A. colonica*), were found at the more stable sites, which were also the smaller, lower gradient streams.

The results indicate that several physico-chemical parameters are involved in the structuring of South Westland stream invertebrate communities, and that no one parameter is of overriding importance. In fact, many taxa have very wide distributions and occur in streams varying considerably in size and with a wide range of physico-chemical and stability characteristics. Particularly notable in this respect are 2 mayfly nymphs - *Deleatidium*, *Nesameletus*, tipulid larvae - *Aphrophila* and *P. skusei*, cased caddisfly larvae *O. feredayi* and Elmidae.

REFERENCES

COWIE, B. (1980) Community dynamics of the benthic fauna of a West Coast stream ecosystem. Ph.D thesis, Univ. of Canterbury.

ELLIOTT, J.M. (1977) Some methods for the statistical analysis of benthic invertebrates. Scientific Publication, Freshwater Biological Association No. 25, 2nd edition.

FISHER, R.A. (1936) The use of multiple measurements in taxonomic problems. *Annals of Eugenetics* 7: 179-188.

GITTINS, R. (1979) Ecological applications of canonical analysis. p. 309-535. *In Statistical Ecology* 7. Ed. by Orloci, L., C.R. Rao & W.M. Stiteler. International Co-operative Publishing House, Maryland, U.S.A.

HOTELLING, H. (1936) Relations between two sets of variates. *Biometrika* 28: 321-377.

PFANKUCH, D.J. (1975) Stream reach inventory and channel stability evaluation. U.S. Dept. of Agriculture. Montana, U.S.A.

ROUNICK, J.S. & M.J. WINTERBOURN. (1982) Benthic faunas of forested streams and suggestions for their management. *New Zealand Journal of Ecology* 5: 140-150.

SOKAL, R.R. & C.D. MICHENER. (1958) A statistical method for evaluating systematic relationships. *University of Kansas, Scientific Bulletin* 38: 1409-1438.

SORENSEN, T. (1948) A method of establishng groups of equal amplitude in plant sociology based on similarity of species content and its application to analysis of the vegetation on Danish commons. Biol. Skr. 5: 1-34.

WARD, J.H. (1963) Hierarchial grouping to optimize an objective function. *Journal of the American Statistical Association* 58: 236-244.

APPENDIX TWO

| Verh. Internat. Verein. Limnol. | 23 | 1422–1426 | Stuttgart, ■ 1987 |
|---|---|---|---|

# Invertebrate drift in three flood-prone streams in South Westland, New Zealand

A. K. GRAESSER

With 3 figures and 2 tables in the text

The ecological roles of stream drift, the downstream movement of benthic invertebrates, are not clearly understood. Catastrophic drift occurs as a result of severe habitat disturbance, often resulting from flooding whereas behavioural drift may be a mechanism for the redistribution of stream benthos in response to both abiotic and biotic factors (WATERS 1972). Alternatively, MULLER's (1974) colonization cycle hypothesis proposed that drift was a density-dependent behaviour which helped maintain populations below the carrying capacity of the stream.

In South Westland, New Zealand, rainfall is high and streams experience rapid and frequent fluctuations in specific discharge. Unpredictable flow regimes and unstable streambeds result in a frequently perturbed environment in which benthic invertebrate populations of low to moderate densities persist. Under such conditions catastrophic drift might be expected to be a frequent occurrence. Results of a study of drift in 3 small streams in South Westland are reported in this paper.

## Study area and methods

Noone, Mapourika and Jetty Creeks are located in the lake Mapourika — Okarito River catchment (NZMS1 S71, 43 ° 19′ S, 170 ° 13′ E), in the South Island of New Zealand. They lie in a region of high rainfall (mean annual rainfall at Franz Josef 20 km S is 4971 mm; 177 raindays a year) and have highly fluctuating discharge regimes. Physico-chemical conditions of the 3 streams are summarized in Table 1. All 3 streams are acidic with moderate concentrations of dissolved organic carbon. Differences in water temperature regimes reflect degree of riparian canopy closure.

Noone Creek has a well-defined stream channel and bed materials are mainly cobbles, pebbles and gravel. The bed of Mapourika Creek consists of numerous pools of fine sediments connected by small cascades composed of moss covered boulders and cobbles. Jetty Creek in contrast to Noone and Mapourika Creeks has a poorly defined stream channel and water flows in an ill-defined manner over a series of cascades and between compacted boulders and cobbles.

Drift was sampled at approximately 2 monthly intervals on 10 occasions between November, 1984 to March, 1986. Sampling was undertaken simultaneously at the 3 sites with nets being emptied before sunset and after sunrise on 2 consecutive days. On each occasion 5 benthic samples were also taken from each stream with a SURBER sampler (0.1 $m^2$, 250 $\mu$m mesh).

Drift nets (250 $\mu$m mesh; 1.2 m long; 7 × 25 cm mouth; 1 net per stream) were placed in areas of rapid flow with the opening just below the water surface. Water velocity and depth were measured

Table 1. A summary of physico-chemical conditions in the 3 study streams, South Westland, November 1984, March — 1986 [mean (1 SD) n = 12 sampling occasions].

| | Noone | Mapourika | Jetty |
|---|---|---|---|
| Discharge ($l \cdot s^{-1}$) | 45 (19.8) | 83 (55) | 19 (15) |
| Stream width (m) | 1.2 (0.2) | 2.3 (0.7) | 0.8 (0.6) |
| Channel gradient (°) | 1 | 9 | 24 |
| Temperature range (°C) | 4–12 | 4–17 | 4–19 |
| pH | 5.7 (0.3) | 6.0 (0.4) | 4.7 (0.2) |
| DOC ($g \cdot m^3$) | 7.0 (2.2) | 4.6 (1.2) | 5.6 (1.9) |

when nets were emptied. Discharge was calculated from multiple measurements of stream width, water velocity and depth. Samples were preserved in 70% ethanol and animals were sorted, identified and counted at ×40 magnification.

## Results and discussion

Composition of the drift was similar at all sites. Terrestrial and emerging aquatic invertebrates were always present and on average made up 30% of the animals collected. They were mainly Collembola, Arachnida and adult Diptera and Hymenoptera. Composition of the invertebrate drift in the 3 streams is summarized in Table 2. *Deleatidium* (Ephemeroptera: Leptophlebiidae) and larval Chironomidae were the most frequently recorded aquatic invertebrates collected in drift samples.

Benthic invertebrate standing crops were low in all streams (mean annual densities (nos/m²): Noone 1300, Mapourika 650 and Jetty 500) and the percentage of the benthos in the drift [calculated using ELLIOTT's (1967) method] was always low; maximum recorded was 0.009%. Drift samples collected at dusk often contained few animals (less than 0.001% of the benthic fauna). Such values were an order of magnitude lower than found by DEATH (1986) in a similar-sized, but less flood-prone stream on the eastern slopes of the Southern Alps. Nevertheless the percentage of benthic invertebrates in the drift at any one time was similar to that reported in a variety of streams elsewhere (e.g. ELLIOTT 1967, BISHOP & HYNES 1969).

Fluctuations in numbers of drifting *Deleatidium* and the other more common aquatic taxa could not be correlated with changes in benthos density: thus it is unlikely that drift was density-dependent. Drift may result in some mortality and redistribution of benthic invertebrates, and limited behavioural drift in conjunction with other directional movements must bring about small-scale dispersion. As many New Zealand aquatic insects are either multivoltine or have relatively aseasonal life history patterns (DEVONPORT & WINTERBOURN 1976, TOWNS 1983, 1985), winged adults are present for much of the year. Therefore continual colonization of streams through oviposition also can be expected to play an important role in maintaining populations of some species in these physically harsh environments.

Drift densities recorded from the 3 streams in January 1985 are shown in Fig. 1. These data are representative of most sampling periods and indicate that more *Deleatidium* nymphs and other aquatic invertebrates were drifting at night than during the day (WILCOXON matched pairs test $z = -3.22, -4.28$, $p < 0.01$).

Table 2. Composition of invertebrate drift in the 3 study streams (mean percentages of all samples combined).

| | Noone | Mapourika | Jetty |
|---|---|---|---|
| Terrestrial arthropods | 53.2 | 37.5 | 18.1 |
| Aquatic invertebrates | 46.8 | 62.5 | 81.9 |
| *Deleatidium* (Eph.) | 10.4 | 10.4 | 13.5 |
| Chironomidae | 10.0 | 15.2 | 37.0 |
| Hydrobiosidae | 2.5 | 3.7 | 3.7 |
| Hydrophilidae | 2.1 | 2.4 | 4.6 |
| *Zelandobius confusus* (Plec.) | 1.4 | 1.7 | 0.6 |
| *Oxyethira albiceps* (Trich.) | 1.1 | – | 0.6 |
| *Zelolessica chiera* (Trich.) | 1.5 | – | – |
| *Coloburiscus humeralis* (Eph.) | 4.2 | – | – |

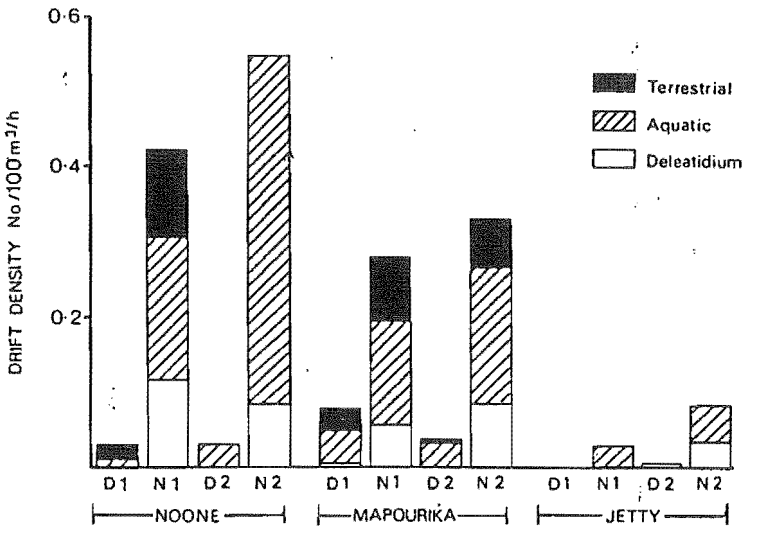



Fig. 1. Drift densities of *Deleatidium*, other aquatic invertebrates and terrestrial invertebrates recorded from the 3 streams in January, 1985.

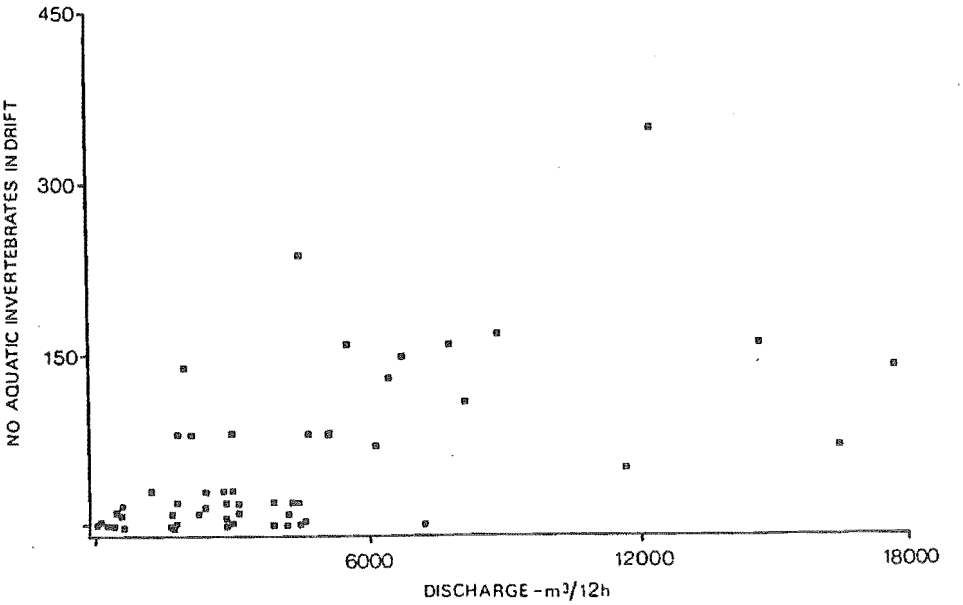



Fig. 2. Number of aquatic invertebrates in night drift samples in relation to discharge.

Numbers of *Deleatidium* and other aquatic invertebrates taken in drift samples were significantly different between sites (FRIEDMAN's nonparametric 2-way ANOVA $\chi^2 = 23.45, 17.39$, $k = 3$, $n = 9$, $p < 0.01$) and were highest at Noone Creek and lowest at Jetty Creek. However, site differences were not found when drift densities (numbers of invertebrates/100 m³/h) were compared.

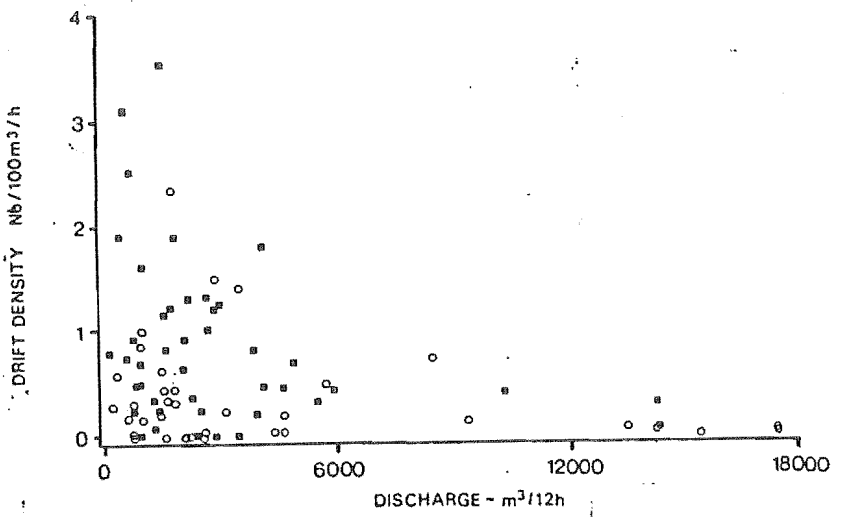



Fig. 3. Drift densities of aquatic invertebrates in night and day samples in relation to discharge (○ — day, ■ — night).

Although drift densities varied from month to month within the range 0—3 invertebrates/100 m³/h, no seasonal patterns were apparent. Instead, temporal differences appeared to be influenced strongly by flow conditions immediately before and at the time of sampling. Numbers of invertebrates drifting increased with discharge (Fig. 2, day $r_s = 0.56$; night $r_s = 0.75$; $n = 60$, $p < 0.01$). However, drift densities decreased with increasing discharge (Fig. 3).

Interpretation of these results is not easy, however, without knowledge of the effect of flow on the drift distances of benthic invertebrates, as this determines the effective source of benthos being sampled. If drift distances do not vary with discharge, then an increase in numbers of invertebrates in the drift can be taken to indicate catastrophic drift. However, if drift distances and velocity are directly proportional as found by ELLIOTT (1971) with some Northern Hemisphere mayfly species and other aquatic insects, then drift density may be a better measure with which to assess the drift response of benthic invertebrates to changes in flow. Thus descreasing drift densities with increasing discharge as found in this study would suggest that invertebrates may actively avoid entering the water column under periods of increasing discharge, perhaps by going deeper into the substratum. Further work on drift distances of benthic invertebrates under varying flow conditions is necessary to validate this hypothesis.

## Acknowledgements

I thank the N. Z. Forest Service and Department of Zoology, University of Canterbury for financial support of this study and the Forest Research Institute for use of their Okarito field station.

## References

BISHOP, J. E. & HYNES, H. B. N., 1969: Downstream drift of the invertebrate fauna in a stream ecosystem. — *Arch. Hydrobiol.* 66: 56—90.

DEATH, R. G., 1986: The cave of Cave Stream: its effect on the invertebrate stream fauna. — Unpubl. B. Sc. (Hons) thesis, Univ. of Canterbury, Christchurch, New Zealand, 65 pp.

DEVONPORT, B. F. & WINTERBOURN, M. J., 1976: The feeding relationships of two invertebrate predators in a New Zealand river. — *Freshwater Biol.* 6: 167—176.

ELLIOTT, J. M., 1967: Invertebrate drift in a Dartmoor stream. — *Arch. Hydrobiol.* 63: 202—237.

— 1971: The distances travelled by drifting invertebrates in a Lake District stream. — *Oecologia (Berl.)* 6: 350—379.

MULLER, K., 1974: Stream drift as a chronobiological phenomenon in running water ecosystems. — *Ann. Rev. Ecol. Syst.* 5: 309—323.

TOWNS, D. R., 1983: Life history patterns of six sympatric species of Leptophlebiidae (Ephemeroptera) in a New Zealand stream and the role of interspecific competition in their evolution. — *Hydrobiologia* 99: 37—50.

— 1985: Life history patterns and their influence on monitoring invertebrate communities. — Biological monitoring in Freshwaters. *Water & Soil Misc. Publ.* 83: 379 pp.

WATERS, T. F., 1972: The drift of stream insects. — *Ann. Rev. Entomol.* 17: 253—272.

Author's address:

Department of Zoology, University of Canterbury, Private Bag, Christchurch, New Zealand

# APPENDIX THREE

## FIELD EXPERIMENTS

### A. Preference of invertebrate grazers for "grazed" and "ungrazed" epilithon

Introduction:

Trials were carried out to determine whether the invertebrate grazer, *Helicopsyche poutini* (Trichoptera: Helicopsychidae) showed any preference for feeding on "grazed" or "ungrazed" tiles collected from Noone Creek.

Materials and Methods:

Larvae of *H. poutini*, a common grazer in Noone Creek, were used in feeding experiments on the additional "grazed" and "ungrazed" tiles. Final and penultimate instar larvae were kept at 4 °C and starved for 24 hours prior to the beginning of an experiment. Pairs of tiles (one grazed", one "ungrazed") were placed side by side (a longitudinal edge) in 3 streamwater filled trays (20x 20x 10cm). Ten larvae were introduced to each experimental chamber in the centre of the the joined longitudinal edge and their positions were recorded at hourly intervals for 3 hours. Each experiment was run in the dark at night when larvae were known to be most active and presumably feeding (pers. observation), and at ambient stream water temperature. A red light was used to locate larvae with minimal disturbance (Elliott 1968). This procedure was repeated on 3 occasions: July, September and November 1986.

Results and Conclusions

On all three occasions, *H. poutini* larvae were equally likely to be found on ungrazed as grazed tiles (Table 1), suggesting that they were opportunistic grazers and would feed on whatever material was available to them.

**Table 1.** Number of *Helicopsyche poutini* larvae on "grazed" and "ungrazed" tiles recorded after 3 hours in July, September and November 1986. Three pairs of tiles were used at each occasions. ns indicates $p > 0.05$

| | "Grazed" tiles | "Ungrazed" tiles | Chi-square test |
|---|---|---|---|
| July | 42 | 48 | 0.40, ns |
| September | 51 | 39 | 1.20, ns |
| November | 44 | 46 | 0.05, ns |

B. Effect of substrate size on invertebrate colonization

Introduction:

During routine sampling of cobble dwelling invertebrates, I observed that "large" cobbles had higher invertebrate densities and taxon richness than "small" cobbles and it was suggested that substrate size may reflect substrate stability during high flow periods. A field experiment was run to investigate the effect of substrate size on invertebrate colonization.

Materials and Methods:

Effect of substrate size on short term colonization patterns of invertebrates was investigated at Noone Creek. Experimental substrates were concrete blocks of two sizes, whole bricks (20x 10x 10 cm) and half

bricks (10x 10x 10 cm), some of which were also "conditioned" prior to the commencement of an experiment to examine whether the presence of epilithon influenced invertebrate colonization. Conditioning involved placing half the bricks of each size class into the stream for 1 month after which time there was a clearly visible difference in their "colour" and texture compared with "unconditioned" substrates.

On 2 occasions (March and May 1986), "unconditioned" and "conditioned" substrates were placed in a section of stream with uniform flow and depth (0.15-0.25 $m.sec^{-1}$ and 10-20cm). Ten bricks of each size class/type were removed from the stream after 2 months (ie. collected in May and July 1986) and all invertebrates colonizing them were identified and counted.

Results and Conclusions:

Table 1 lists the mean invertebrate densities of the four treatments recorded in May and July 1986. On both occasions, no differences in invertebrate densities or taxon richness were found between "large" and "small" substrates, however, invertebrate densities on "conditioned" and "unconditioned" substrates were significantly different (Kruskal Wallis= 30.16, 29.49, df=3 for May and July 1986, respectively).

Table 1. Mean invertebrate densities and taxon richness in parentheses of the four treatments: "conditioned" and "unconditioned", "large" and "small" substrates, recorded in May and July 1986. For each treatment, n= 10. Density = numbers per brick.

| | Large, unconditioned substrates | Large, conditioned substrates | Small, unconditioned substrates | Small, conditioned substrates |
|---|---|---|---|---|
| May | 11.4 (8) | 32.5 (16) | 9.5 (3) | 28.5 (8) |
| July | 9.9 (3) | 29.8 (9) | 11.1 (2) | 31.1 (9) |

In these trials, similar invertebrate colonization patterns were observed for the two sizes of substrate suggesting that under "normal" flow conditions, the stability of these substrates was similar and invertebrates were able to tolerate the flow conditions associated with both sizes of substrate. Moreover, conditioning of substrates increased invertebrate densities and taxon richness suggesting that the epilithon on the substrates provided the invertebrates with a more "natural" habitat.

References:

ELLIOTT, J.M. (1968) The daily activity patterns of mayfly nymphs (Ephemeroptera). *Journal of Zoology (London)* 160: 279-290.